...useums
H
A6

The American Midland Naturalist

Devoted to Natural History, Primarily that of the Prairie States

Founded by J. A. Nieuwland, C.S.C.

Contents

Bryophytic Unions of Certain Forest Types of the Great Smoky Mountains—*Stanley A. Cain* and *Aaron J. Sharp* 249

Bark Factors Affecting the Distribution of Corticolous Bryophytic Communities—*W. D. Billings* and *W. B. Drew* 302

Notes on Plantago in the Pacific States—*Louis C. Wheeler* 331

Creosote Bush and the Lower Sonoran Zone of the Southwest—*Joseph Ewan* 334

Some Blood Parasites from Birds of the Lake Okaboji Region—*G. Robert Coatney* 336

The North American Fresh-Water Tetraonchinae—*John D. Mizelle* and *R. Chesler Hughes* 341

Nine New Thysanoptera from North America—*J. Douglas Hood* 354

Descriptions of New Ants from the Western United States—*A. C. Cole, Jr.* 368

Contributions to Texan Herpetology VII. The Salamanders—*Charles E. Burt* 374

A Systematic Account of the Alligator Lizards (Gerrhonotus) in the Western United States and Lower California—*Henry S. Fitch* 381

The Biotic Districts of Oklahoma—*W. F. Blair* and *T. H. Hubbell* 425

Notes on the Den Ecology of the Striped Skunk in Iowa—*Lyle F. Selko* 455

Breeding of the Cottontail Rabbit in Southern Michigan—*Durward L. Allen* 464

Book Reviews 470

Vol. 20 SEPTEMBER, 1938 No. 2

EDITORIAL STAFF

THEODOR JUST,.....*Botany (Ecology, Taxonomy)*
Editor, University of Notre Dame

CARROLL LANE FENTON,.....*Invertebrate Paleontology*
Washington, D. C.

JOHN HOBART HOSKINS,.....*Botany (Morphology, Paleobotany)*
University of Cincinnati, Cincinnati, Ohio

REMINGTON KELLOGG,.....*Vertebrate Paleontology and Zoology*
U. S. National Museum, Washington, D. C.

MARCUS WARD LYON, JR.,.....*Mammalogy*
South Bend, Indiana

GEORGE WILLARD MARTIN,.....*Mycology*
State University of Iowa, Iowa City, Iowa

FRANCIS JOSEPH WENNINGER, C.S.C.,.....*Invertebrate Zoology*
University of Notre Dame

NOTE:—THE AMERICAN MIDLAND NATURALIST, published from the biological laboratories of the University of Notre Dame, is primarily, though not exclusively devoted to the Natural History of the Middle West. A wide selection of papers on botany, paleontology and zoology is published in bi-monthly issues, six of which make up a volume.

Fifty reprints will be furnished free of charge to contributors. Additional reprints should be ordered when proof is returned and may be had at cost price. Authors are requested to submit abstracts with their manuscripts.

The following numbers are out of print: vol. 2. (1-3, 8-10); vol. 3, (1-3, 5-12) index, title page; vol. 4, (1-7) index, title page; vol. 6, (5, 8) index, title page; vol. 9, (9); vol. 10, index, title page; vol. 11, (1). All others available, 30 cents per copy. Complete volumes: $3.00; volumes 7, 13, and 14, $1.50 each; vol. 15 $2.00, single issues 35 cents; vol. 16 $3.00, single issues 50 cents; vol. 17 $4.50, part 1 $2.00, nos. 2-6 50 cents each; vol. 18 $3.00, single issues 50 cents; vol. 19 $2.50, vol. 20 $2.50, single issues $1.00.

Exchanges for journals, special volumes or duplicate books, and specimens, should be arranged directly through the editorial office at the University of Notre Dame, where subscriptions also are received. Offers should accompany request for exchange.

For citation use this abbreviation: *Amer. Midl. Nat.*

Entered as second-class matter at Notre Dame, Indiana. Acceptance for mailing at special rate of postage provided for in section 1103, Act of October 3, 1917, authorized on July 3, 1918.

The American Midland Naturalist

Published Bi-Monthly by The University of Notre Dame, Notre Dame, Indiana

VOL. 20 SEPTEMBER, 1938 No. 2

Bryophytic Unions of Certain Forest Types of the Great Smoky Mountains[1]

Stanley A. Cain and Aaron J. Sharp

TABLE OF CONTENTS

I. INTRODUCTION 250

II. LITERATURE 254
- A. Taxonomy and general distribution 254
- B. Ecological bryo-geography 254
- C. Bryophytic components of other communities 255
  - 1. Correlations with higher associations 255
  - 2. Forest site-types 255
- D. Studies of bryophytic "associations" per se 256
- E. Phytosociological descriptions of bryophytic communities 256
- F. Bryo-ecology 257
- G. Successions of bryophytes (dynamics) 258
- H. General Works 259

III. METHODS 259
- A. Terrestrial communities 260
- B. Epilithic communities 262
- C. Epixylic communities 263
- D. Corticolous communities 263
- E. Statistical classes 265

IV. RESULTS 265
- A. Bryophytic communities of the subalpine forest types 265
  - 1. Abietum Fraseri 266
  - 2. Piceetum rubentis 271
  - 3. Fagetum grandifoliae subalpinum 276
- B. Bryophytic communities of the cove hardwood forest types 278
  - 1. Aesculo-Tilietum 279
  - 2. Halesio-Saccharodendretum 284
  - 3. Liriodendro-Tsugetum 288

V. DISCUSSION 295
- A. Recognition and delimitation of communities 295
  - 1. Upper corticolous communities 295
  - 2. Communities of large pleurocarpous mosses 297

VI. REFERENCES 299

1 Contributions from the Botanical Laboratory, The University of Tennessee, n. ser. 24, and The Waterman Institute, Indiana University, contrib. no. 80. The field work for this paper was done in 1935 while the senior author was Research Associate of the Waterman Institute. The manuscript has been prepared by the authors who are now both at The University of Tennessee.

I.—Introduction

Bryocoenological work in America is in its infancy; in fact, practically no studies on bryophytic communities were made according to modern methods. This situation is mainly due to the fact that most ecologists pass over the cryptogamic elements in the flora of complex communities, such as forest associations, because of unfamiliarity with the taxonomy of mosses and liverworts. On the other hand, the bryologists were busy for most part with purely floristic and taxonomic problems. Consequently bryophytic communities received little more than passing attention. The solution of these difficulties lies, probably, in cooperative work between plant sociologists and bryologists.

The senior author has been working on the forest associations of the Great Smoky Mountains for the past few years and now has near completion studies on several of the virgin forest types. The junior author has been studying the bryophytes of the same region for an equal length of time, but only recently has the joint project reported in this paper been undertaken.

The six forest associations here considered may be classified as follows:

Prealpine belt: The Canadian spruce-fir forest
Abietum Fraseri—The southern balsam fir association
Piceetum rubentis—The red spruce association
Fagetum grandifoliae subalpinum—The beech gap association

Montane belt: The cove hardwoods forest
Aesculo-Tilietum—The buckeye-basswood association
Halesio-Saccharodendretum—The peawood-sugar maple association
Liriodendro-Tsugetum—The yellow poplar-sugar maple association.

All the important bryophytic communities of each of these forest associations have been studied at one station for each association. The bryophytic communities were studied on a basis of their substrata, according to the following groups:

Terrestrial communities—the soil layer (Bodenschicht)
Epilithic communities—on erratic boulders and cliffs
Epixylic communities—on fallen logs without bark
Corticolous communities:

tree-butt communities—up to a height of 1 to 2 meters
tree trunk communities—on the main bole
top-limb flora—on the small branches of the canopy.

The bryophytic flora of the region is very rich, both in species and in communities. The communities described in this paper are those characteristic of the forest associations at the stations investigated. It is recognized, of course, that intensive studies of delimited stations do not form an adequate basis for generalizations relative to the bryophytic communities of the forest associations as they occur elsewhere. It is our impression, however, that the most extensive communities of these stations are typical of the associations in the Great Smoky Mountains region, and to a certain extent elsewhere. It remains for further work to show how uniform the bryophytic communities

of these forest types are over the whole range of the forest associations concerned.

Our statistical analyses of the bryophytic communities encountered led to the description in the tables of 34 communities. Only a portion of the tabulated communities, however, was given a definite status (see the discussion). Such assignment involves community nomenclature and taxonomy, a matter discussed in the following paragraphs.

Several European plant sociologists described associations composed solely or almost exclusively of cryptogams, and hence one-layered. These associations in some instances were regarded as of equal rank with other associations which are many layered. Such treatment produces considerable quantitative divergence between the simple one-layered associations and the very complex phytocoenoses which are the more common associations. Several solutions to the problems involved in the complexity of vegetational classification were proposed. Lippmaa (1934, 1935), for example, proposed the *unistratal association concept* in which each stable synusia of a phytocoenosis is considered as being more or less independent and in consequence an "association." This concept was considered in the following American papers: Cain (1936), Cain and Penfound (1938), Gleason (1936). The extreme position of Lippmaa was not accepted; in fact, it was voted down at the Amsterdam Congress where it was decided not to call such synusial communities associations. The name settled upon for such communities is that of "union" (Sirgo, 1937). Thus a forest association (phytocoenosis) may consist of several unions. The first American study using such a designation is that by Cain and Penfound (1938) on the red maple swamp forest association of Central Long Island in which the following components of this association were described:

Aceretum rubri—The red maple swamp forest association
Acer rubrum union—the arborescent layer
Clethro-Azalea union—The frutescent layer
Rubus hispidus union—an herbaceous (field) layer
Unifolium canadense union—an herbaceous layer
Spathyema foetida union—an herbaceous layer
Homomallium adnatum union—a cryptogamic synusia on trees
Dicranum montanum union—a cryptogamic synusia on peat, and several other bryophytic unions.

In the present paper, dealing only with bryophytic communities, we too decided to use the designation "union." Thus, we described a widespread community dominated by *Thuidium delicatulum*. It is merely called "the *Thuidium delicatulum* union" and is not given the more technical name, *Thuidietum delicatulae,* because of the probable confusion with association names. However, it seemed feasible to indicate the "alliances" which these unions form. Thus we have the Neckero-Ulotion, an alliance of three unions and four facies, and the Thuidion delicatulae, an alliance of seven unions and ten facies. Apparently no good objection can be raised to such a procedure, although the term "alliance" and the termination "-ion" are usually applied to floristically related groups of associations, not unions.

In some instances we designated certain very closely related communities

of subordinate rank as "facies" of a certain union. The conspicuous example of such treatment is the case of the communities dominated by species of *Hypnum* (using *Hypnum* in the broad sense). These communities are all considered to belong in the same union, i.e. collectively to constitute the *Hypnum* union. Specifically, each of several ecologically equivalent species may locally dominate a stand and thus form a facies of the union. Thus:

Hypnum union (collective sense)	Heterophyllum nemorosum facies
Hypnum imponens facies	Brotherella recurvans facies
H. fertile facies	B. delicatula facies
H. curvifolium facies	Bazzania trilobata facies

In the recent paper by Bizot (1937) we have a precedent for considering the *Hypnum* species collectively. He speaks of "Hypnacées sylvatiques, abundance 4" for all forest species of *Hypnum* in a certain region on shaded rocks.

An alphabetical check list of the Bryophyta reported in this paper follows below. The names of the Hepaticae follow Buch, Evans, and Verdoorn 1937 (1938). The moss names follow Grout (1928-37) insofar as that work is completed, otherwise Grout (1903). Only in the following list are the name authorities given.

BRYOPHYTA

HEPATICAE (Liverworts)

1. *Bazzania denudata* (Torr.) Trevis
2. *B. nudicaulis* Evans
3. *B. trilobata* (L.) S. F. Gray
4. *Blepharostoma trichophyllum* (L.) Dum.
5. *Calypogeia fissa* (L.) Raddi
6. *C. suecica* (Arn. & Pears.) C. M.
7. *Cephalozia ambigua* C. Massal.
8. *C. bicuspidata* (L.) Dum.
9. *C. curvifolia* (Dicks.) Dum.—*Nowellia curvifolia* (Dicks.) Mitt.
10. *C. media* Lindb.
11. *Cephaloziella spinicaulis* Douin
12. *Cololejeunea Biddlecomiae* (Aust.) Evans
13. *Frullania Asagrayana* Mont.
14. *F. eboracensis* Gottsche
15. *Geocalyx graveolens* (Schrad.) Nees
16. *Harpanthus scutatus* (W. & M.) Spruce
17. *Harpolejeunea ovata* (Hook.) Schiffn.
18. *Herberta tenuis* Evans
19. *Jamesoniella autumnalis* (D. C.) Steph.
20. *Jubula pennsylvanica* (Steph.) Evans
21. *Lejeunea patens* Lindb.
22. *Lepidozia reptans* (L.) Dum.
23. *Leucolejeunea clypeata* (Schwein.) Evans
24. *Lophocolea heterophylla* (Schrad.) Dum.
25. *Lophozia incisa* (Schrad.) Dum.
26. *Metzgeria conjugata* Lindb.
27. *M. crassipilis* (Lindb.) Evans
28. *M. furcata* (L.) Dum.
29. *M. hamata* Lindb.
30. *M.* sp.
31. *Microlejeunea laetevirens* (Nees & Mont.) Evans
32. *M. ulicina* (Tayl.) Evans
33. *M.* sp.
34. *Mylia cuneifolia* (Hook.) S. F. Gray
35. *Plagiochila tridenticulata* Tayl.
36. *P.* sp.
37. *Porella platyphylloidea* (Schwein.) Lindb.
38. *Radula caloosiensis* Aust.
39. *R. Sullivantii* Aust.
40. *R.* sp.
41. *Riccardia palmata* (Hedw.) Carruth.
42. *Scapania nemorosa* (L.) Dum.
43. *S. undulata* (L.) Dum.
44. *Sphenolobus exsectus* (Schmidt.) Steph.—*Tritomaria exsecta* (Schmidt.) Schiff.
45. *S. Michauxii* (Web.) Steph.—*Anastrophyllum Michauxii* (Web.) Buch

MUSCI (Mosses)

1. *Amblystegium serpens* (L., Hedw.) Bry. Eur.
2. *A. varium* (Hedw.) Lindb.
3. *Anacamptodon splachnoides* (Froehl.) Brid.
4. *Anomodon attenuatus* (Schreb., Hedw.) Hueben.
5. *A. rostratus* (Hedw.) Schimp.
6. *A. Rugelii* (C. Muell.) Keisel.
7. *A. tristis* (Cesati) Sull.
8. *Brachythecium oxycladon* (Brid.) Jaegr. & Sauerb.
9. *B. plumosum* (Sw.) Br. & Sch.
10. *B.* sp.
11. *Brotherella delicatula* (James) Fleisch.
12. *B. recurvans* (Michx.) Fleisch.
13. *Bryhnia novae-angliae* (Sull. & Lesq.) Grout
14. *Campylium chrysophyllum* (Brid.) Bryhn
15. *Calliergonella Schreberi* (Willd., Bry. Eur.) Grout
16. *Cirriphyllum piliferum* (Schreb.) Grout
17. *Dicranella heteromalla* (L., Hedw.) Schimp.
18. *Dicranodontium denudatum* (Brid.) E. G. Britt.
19. *Dicranum fulvum* Hook.
20. *D. fuscescens* Turn.
21. *D. montanum* Hedw.
22. *D. scoparium* (L.) Hedw.
23. *Diphyscium sessile* (Schmid.) Lindb.
24. *Drummondia prorepens* (Hedw.) Jennings
25. *Entodon brevisetus* (Hook. & Wils.) Jaegr. & Sauerb.
26. *Eurhynchium serrulatum* (Hedw.) Kindb.
27. *Fissidens cristatus* Wils.
28. *F. minutulus* Sull.
29. *F. subbasilaris* Hedw.
30. *Grimmia apocarpa* var. *gracilis* (Schleich) Web. & Mohr.
31. *G. pilifera* Beauv.
32. *Hedwigia ciliata* (Ehrh.) Hedw.
33. *Heterophyllum nemorosum* (Koch) Kindb.
34. *Homalotheciella subcapillata* (Hedw.) Card.
35. *Homomallium adnatum* (Hedw.) Broth.
36. *Hylocomium brevirostre* (Ehrh., P. B.) Bry. Eur.
37. *H. splendens* (Hedw.) Bry. Eur.
38. *H. umbratum* (Ehrh., Hedw.) Bry. Eur.
39. *Hypnum Crista-castrensis* L., Hedw.
40. *H. curvifolium* Hedw.
41. *H. fertile* Sendt.
42. *H. imponens* Hedw.
43. *H. molluscum* Hedw.
44. *H. reptile* Michx.
45. *Leptodon trichomitrion* (Hedw.) Mohr.
46. *Leptodontium excelsum* (Sull.) E. G. Britt.
47. *Leucobryum glaucum* (L.) Schimp.
48. *Leucodon brachypus* Brid.
49. *L. julaceus* (Hedw.) Sull.
50. *L. sciuroides* (L., Hedw.) Schwaegr.
51. *L.* sp.
52. *Mnium affine* var. *ciliare* (Grev.) C. M.
53. *Neckera pennata* (L.) Hedw.
54. *Orthotrichum pumilum* Dicks.
55. *O. stellatum* Brid.
56. *Paraleucobryum longifolium* (Hedw.) Loesk.
57. *Plagiothecium deplanatum* (Sull.) Grout
58. *P. laetum* Bry. Eur.
59. *P. micans* (Sw.) Paris
60. *P. Muellerianum* Schimp.
61. *P.* sp.
62. *Platygyrium repens* (Brid.) Bry. Eur.
63. *Pohlia elongata* Hedw.
64. *Polytrichum Ohicense* R. & S.
65. *Porotrichum allegheniense* (C. M.) Grout
66. *Rhodobryum roseum* (Weis.) Limp.
67. *Rhytidiadelphus triquetrus* (L., Hedw.) Warnst.
68. *Schwetschkeopsis denticulata* (Sull.) Broth.
69. *Sematophyllum carolinianum* (C. Muell.) E. G. Britt.
70. *S. adnatum* (Michx.) E. G. Britt.
71. *Sphagnum Girgensohnii* Russ.
72. *S. imbricatum* var. *affine* (R. & C.) Hornsch.
73. *S. squarrosum* Pers.
74. *Tetraphis pellucida* Hedw.
75. *Thuidium delicatulum* (L., Hedw.) Mitt.
76. *Trichostomum cylindricum* (Bruch) C. Muell.
77. *Ulota americana* (P. B.) Limpr.
78. *U. americana* var. *rufescens* (E. G. Britt.) Paris
79. *U. crispa* (Hedw.) Brid.
80. *Zygodon viridissimus* (Dicks.) Brown
81. *Z.* sp.

II. Literature

There is no occasion for an extensive consideration in this paper of the literature of bryocoenology. It seems worthwhile, however, to mention some papers representative of certain types of studies, although none of them applies specifically to the bryocoenology of the Great Smoky Mountains region. Such papers do, however, form a background and they, of course, tempered the approach of the authors to their work.

A. Taxonomy and General Distribution

The bulk of the bryological literature naturally treats of taxonomic and general problems of distribution: monographs, manuals, floras. There are numerous notes in the journals concerning unusual occurrences, relict colonies, and disjunct distributions for all countries which have been extensively botanized. In the United States, in fact, little other bryological literature is available.

B. Ecological Bryo-Geography

In the last three or four decades numerous papers appeared dealing with the bryology of natural areas and types of substrata of certain regions. Amann's (1896) early paper, "Étude de la Flore Bryologique du Haut-Jura Moyen," is typical of these. He listed the bryophytes of different altitudinal belts and for such habitats as: dry stations and humid gorges of low elevations; calcicoles and calcifuges of montane regions; shaded rocks, forests, dead wood, erratic boulders, etc. His book, "Bryogéographie de la Suisse" (Amann, 1928), represents the culmination of three decades of such work. The paper by Bizot (1937), "Bryogéographie de la Côte D'Or," is ample evidence that such an approach is still of interest and value. In England, Watson (1932, 1936) has probably done most of the work by listing the species of various habitats, vegetational types, and regions. The papers cited above contain numerous references to his contributions dating from 1909. In the United States the papers by Nichols (1913, 1915, 1916) on the vegetation of Connecticut are about the only ones to give comprehensive consideration to the bryophytic components of the vegetation of a region. The following outline will indicate his disposition of the bryophytic flora into habitat groups:

Virgin forests
- ground, roots, logs or stumps
- rocks and boulders
- trunks of trees
- bases of trees

Lowland plant societies
- submersed or floating
- open sedge or shrub swamps
- wooded swamps
  - wet or moist depressions
  - stumps, logs, etc.

Societies along streams
- aquatics
- more or less hydrophytic
- periodically inundated rock surfaces
- springy banks
- overhanging cliffs and precipitous rocks
  - wet or moist
  - dry
  - calciphiles, calciphobes.

Perhaps two other papers should be cited as examples of this group. That of Koppe (1929) lists the mosses which constitute the montane element in

Schleswig-Holstein by characteristic situations. The other by Lippmaa (1933) lists all the synusial communities of Esthonia, classified on a dual basis of life-form and habitat. The life-form synusiae for the moss-liverwort-lichen communities consist of 21 named associations (unions) for that country.

C. Bryophytic Components of Other Communities

There is another fairly large group of papers the main interest of which is the higher vegetation, but in which the bryophytic elements are given more than the usual slight consideration. Some of these may be mentioned under the following headings:

1. *Correlations with higher associations* (phytocoenoses).—Cooper (1912), in studying succession upon Isle Royale, found definite moss correlations from rock shore to climax forest, and from bog mat to climax forest. The slowness with which changes occur among cryptogams on rocks was demonstrated by his re-examination of the area seventeen years later, Cooper (1928). The dune successions near Lake Michigan, which were made world famous by Cowles, were studied for their bryophytes by Taylor (1920). She tabulates the mosses of the cottonwood, pine, pine-oak, oak and beech-maple stages of the xerosere; and of the open water, sedge, tamarack, swamp forest, and beech-maple stages of the hydrosere. The most detailed study yet to appear in our country of the bryophytic communities of any forest association is that by Cain and Penfound (1938) on the Aceretum rubri of Central Long Island. Many of the papers so far cited, and yet to follow, also illustrate correlations of bryophytes with higher vegetational types.

2. *Forest site-types.*—The classical work of Cajander (1909, 1926) on forest types is based on the characteristic ground vegetation as indicators of site quality, independent of the arborescent overstory. It is held by Cajander that the ground vegetation characterizes biologically equivalent sites. Heimberger (1934) who, in the Adirondack region, made the only thorough application of Cajander's concepts and methods in the United States, gives a complete review of the literature. He states that "the Finnish types, if subdivided according to species of trees, would give units corresponding to those of Sukachev," leader of the Russian school. Heimberger lists 22 forest types in three series. For example, the subalpine series (3200-4900 ft.) with red spruce, balsam fir, white birch, mountain ash, white and black spruce, and yellow birch, is subdivided into three forest types: (1) Hylocomium-Cornus Type; (2) Oxalis-Hylocomium Type; (3) Aspidium-Oxalis Type. A number of characteristic bryophytes of the forest types are listed, of which *Hylocomium splendens, Hypnum Schreberi, H. Crista-castrensis,* and *Sphagnum* are dominant in Type 1. The point which is emphasized here is that this kind of forest-type study takes into consideration the lower synusiae and does not, as in most American forestry, ignore the field and ground layers of shrubs, herbs, and cryptogams. That the method enabled European foresters (and Heimberger in this country) to build up a valuable and practical forest-site classification is due to the fact that many of the inferior species are good indicators of biologically equivalent sites.

The preceding papers pay little attention to epiphytic bryophytes. Two papers may be mentioned especially which record correlations between corticolous bryophytes and forest types: Watson (1936) for British forests; Wisniewski (1929) for certain Polish virgin forest associations.

D. Studies of Bryophytic "Associations" *per se*

A number of botanists studied communities of bryophytes and considered them to be of the rank of association. That is, they treated these one-layered communities on a par with the multi-layered associations. Most plant sociologists did this only when the bryophytic communities occur in the open, i.e. without an overstory. For example, Koppe (1932) describes the *Haplomitrium-Fossombronia incurva*-association on moist sands from 22 stations in the heath-moor region. Markgraf (1926) describes a *Polytrichum strictum*-association also on the moor. When bryophytic communities occur as a component part of a phytocoenosis, it is the usual practice to consider them as "societies." Certain authors, even in such cases, speak of "moss associations." Thus, Wisniewski (1929) describes the following corticolous associations from Polish virgin forests:

I. Epiphytic associations
   1. Association of *Anomodon viticulosus* and *Leucodon sciuroides*
   2. Association of *Drepanium cupressiforme* var. *filiforme* and *Orthodicranum montanum*

II. Associations of the base of the trunks
   3. Association of *Eurhynchium striatum*
   4. Association of *Pleurozium Schreberi*.

In the United States it is the custom to refer to such communities as societies (Emig, 1930). Recently Wilson (1936) described six corticolous associations which form the alliance, Homomallion adnatum. These associations are: Homomallietum adnatum, Platygyrietum repens, Anomodetum tristis, Anomodetum, Schwetschkeopsetum denticulatae, Leskeetum gracilescens. Ochsner (1927) described 18 epiphytic associations of algae, lichens, and bryophytes for Switzerland, grouped in nine alliances. Lippmaa (1933, 1934, 1935) treated all synusial groups as associations on a basis of his unistratal association concept. At present, however, he refers to them as "unions." The same treatment is adopted in the present paper and in that by Cain and Penfound (1938).

E. Phytosociological Descriptions of Bryophytic Communities

Bryologists working with bryophytic communities tended in general toward the use of qualitative descriptions and species lists without quantitative data. Some went a step farther, presenting estimates of abundance which are only as good as the experiences and judgment of the author. Watson (1932) gives estimates of abundance which are of value because of his wide experience and knowledge of bryophytes. Plant sociologists generally attempted more quantitative descriptions, frequently based on quadrat sampling, and presented more or less complete sociological tables. Their results may include data on

local frequence, presence, constance, sociability, fidelity, coverage, life-form. (See Braun-Blanquet, 1932; Braun-Blanquet and Pavillard, 1925; Cain, 1932, for a consideration of these concepts). The Scandinavian phytosociologists employed for most part definitely limited quadrats in their studies. Much of this literature is discussed in DuRietz (1930). A few papers employing the quadrat method may be mentioned. Olsen (1917) studied bryophytic species on trees. He presents tables for various tree species giving the frequency of the mosses on each tree from 25 quadrats each a dm. sq. Kleist (1929) gives complete sociological tables for the bogs near Warsaw, including the bryophytic communities. Gams (1934) presents the first quadrat study in the steppe to consider lower plants. His tables show the local frequence and coverage for the bryophytic species at the various stations investigated. Heimberger (1934), in his study of forest types in the Adirondack region, used series of 25 quadrats of 0.1 sq. m. area to obtain data on the coverage and frequence of the species. Sirgo (1935) gives coverage and sociability data for bryophytic communities. Cain and Penfound (1938) give constancy and coverage data for the bryophytic unions of the red maple swamp forest type.

Especially in dealing with epiphytic communities, several authors used as a unit the entire bryophytic stand of a community on a tree. Ochsner (1927) and Wisniewski (1929) made valuable contributions in this regard. The latter is particularly critical of the quadrat method. He says:

> Constance is noted (French-Swiss method) after the results have been obtained in examining each association-individual and not by freely chosen squares. I have given preference to that method rather than to the Swedish, which pretends to be more exact, but is less precise in reality. What is it that determines the choice of squares? Errors are more easily made when one works with small surfaces. The Swedish method can give satisfactory results only in the case where stands are entirely divided into squares and where all squares are examined. Therefore, why make the division into squares?

F. Bryo-Ecology

Scattered references to bryophytes (and lichens) as indicators of climate are available. For example, Cockayne (1926), speaking of the New Zealand *Nothofagus* forest says:

> When the forest-floor is closely covered with a dense carpet of foliaceous liverworts (species of *Aneura, Plagiochila, Symphogyna, Gottschea, Trichocolea,* etc.), mosses and filmy ferns, and when the tree trunks are similarly clad and every log is covered with translucent, moist greenery, it is a certainty that the rainfall is extremely heavy and rainy days very frequent. The matter has received no detailed study as yet, but it seems highly probable that certain species of bryophytes, and their relative abundance, are admirable indicators of different degrees of rainfall.

Shreve (1914), referring to stratification in a montane rainforest, points out that

> the epiphytes of the lowest level are pronounced hygrophytes, confined to that level by its favoring conditions of humidity and frequent wetness. The mid-level forms are somewhat drought-resistant. . . The epiphytes of the topmost level are pronouncedly xerophilous.

In an earlier paper Shreve (1911) points out that a similar difference exists in the case of the Hymenophyllaceae and that it is determined by the vertical difference between the *climate* of the floor of the forest and its canopy,

a factor which is operative in the case of all epiphytic vegetation. Thus, species in their broad distribution may be indicators of the general climate, and in their restriction to habitat niches, may indicate local or microclimate. There are many references in the literature to such matters as the occurrence of "Atlantic (oceanic) elements" in the flora of the continental interior of Europe (as in Bizot, 1937), or to boreal relicts in somewhat southerly regions (as in Conard, 1932). Such enumerations are more or less direct allusions to extraneous floristic elements as indicators of local climatic conditions which are more or less severe than the general regional climate.

Comparatively little is known on the morphogeny of bryophytes (including polymorphism, species plasticity, adaptations) with respect to measured habitat conditions. The most thorough paper of this type known to the writers is that of Davy de Virville (1927-28). Individual chapters treat of the influence of a certain climatic factor: illumination, temperature, humidity. aquatic habitat, etc. He concludes that:

> There is a strong analogy between the variations of mosses in nature and the modifications which can be provoked artificially in the laboratory.

Several authors studied the ecology of bryophytic communities by direct measurement of habitat factors (atmospheric and edaphic) and by deductions from occurrence, as in exposure on tree trunks, height on the tree, etc. For example hydrogen-ion concentration was studied by Robinove and LaRue (1928), Montgomery (1931), Glenn and Welch (1931), Apinis and Diogucs (1933-35) Ikenberry (1936); light influences were discussed by Olsen (1917), Van Oye (1921), Plitt and Pessin (1924), Pessin (1925), and Wisniewski (1929); and temperature by Pessin and Wisniewski. Relations to liquid water and to atmospheric humidity were studied by most of the authors cited above. Pessin summarized the effects of the atmospheric factors in terms of evaporation (evaporating power of the air). Ochsner (1927) studied the water-absorbing capacity of several bryophytes and lichens and expressed the results by coefficients. Olsen (1917) mentioned the relation of bryophytic occurrence to wind exposure and gave a few figures on osmotic concentration of the cell sap, which ranges up to 40 atmospheres.

With respect to the occurrence of corticolous bryophytes, the effects of atmospheric factors were revealed by correlation with direction of exposure (north, south, etc.), height (tree base, trunk, canopy), slope of tree, isolation, etc.: Van Oye (1921), Ochsner (1927), Cain and Penfound (1938). The influences of the tree species, character of the bark, tree size (age), were discussed by Olsen (1917), Van Oye (1921), Ochsner (1927) and others.

All authors who described the nature of the substratum on which certain bryophytes occur contributed, in a general way, to bryo-ecology.

G. Successions of Bryophytes (Dynamics)

Correlation of bryophytes with the different stages in the succession of higher plants was mentioned previously. The actual succession of one bryophytic community by another is as yet poorly known. Olsen (1917) says

young trees are too smooth for bryophytes. First come acrocarpous species in the small fissures and isolated tufts of *Orthotrichum* and *Ulota*. Pleurocarpous species come later when the rougher bark provides numerous points of attachment, and they rapidly supplant the acrocarpous species, finally covering the entire surface of the stem. Taylor (1920) describes succession on rock surfaces, *Fissidens* being replaced by *Anomodon,* and that in turn by *Thuidium* and *Entodon*. She says that in this third stage "no traces remained of the typical pioneer mosses." Dudgeon (1923), writing on successions among epiphytic communities in the *Quercus incana* forest at Landour, describes six stages: (1) crustose lichen stage on branches 3-4 years old; (2) foliose-fruticose lichen stage (*Usnea barbata,* etc.) 9-12 years, may nearly cover the branches; (3) pioneer moss stage *(Lindbergia, Frullania)* gradually shading out the lichens; (4) climax moss stage *(Leucodon, Diaphanodon, Cryptoleptodon),* forming a thick continuous pad in 20 years under favorable conditions; (5) fern stage; (6) flowering plant stage. Ochsner (1927) describes the following communities on beech trees: (1) Phlyctidetum, dominant when the trees are 40-60 cm. in circumference; (2) Ulotetum, maximum at 60-80 cm. circumference (3) Drepanietum, maximum at 80-100 cm. Cain and Penfound (1938) mention certain successions on peat and soil in the red maple swamp forest.

H. General Works

There are a few books to which the student of bryophytic communities can constantly refer with advantage. The "Geographie der Moose," by Herzog (1926) contains three sections: (1) morphology, autecology, synecology, and climatic and edaphic factors; (2) distribution of bryophytic families and other taxonomic groups; (3) floristic regions. The "Manual of Bryology," edited by Verdoorn (1932), contains several chapters of especial interest: physiology, by Garjeanne; geography, by Herzog; quaternary distribution, and bryocoenology, by Gams; ecology, by Richards. Rübel's (1930) "Pflanzengesellschaften der Erde"; DuRietz's (1930) "Vegetationsforschung auf soziationsanalytischer Grundlage"; Braun-Blanquet's (1932) "Plant Sociology" should not be overlooked for general information concerning plant sociological methods and concepts.

III. Methods

From the preceding section, which provides an introduction to the literature of bryocoenology, it is obvious that students of bryophytic and lichen communities employed a wide variety of methods. In many instances such communities are easily recognized and well-defined. As a consequence, the older and more general methods of community description are frequently adequate, especially when the species list for a community is short and the dominants few and evident. In other instances one wishes that the descriptions available in the literature provided more information regarding the quantitative, qualitative, and ecologic relationships of the component species of the communitiies considered. We endeavored to use methods which yield

data giving adequate pictures of the communities treated without, however, allowing the technique of sampling to usurp the more important place.

It would seem, at this stage at least, that standardization of sampling technique is undesirable in bryocoenology. The great diversity among such communities, especially as found on different substrata, requires individual methods of treatment. Nevertheless, there are certain procedures for certain problems which meet the demands of a more exact description and which, if more widely used, would permit easier comparison of the communities studied by different investigators in different regions. Similar, if not identical, communities are to be met with in widely scattered regions. This is probably true to a greater extent for communities of bryophytes and lichens than it is for communities of phanerogams (except for certain hydrophytic and helophytic communities) because so many of the characteristic species of cryptogams range over comparable parts of North America, Europe and Asia, or are of even wider distribution.

A. Terrestrial Communities

The hardwood forest types studied *(Liriodendro-Tsugetum, Halesio-Saccharodendretum, Aesculo-Tilietum,* and *Fagetum grandifoliae subalpinum)* in the virgin, climax condition showed little or no development of terrestrial bryophytic communities. This is due to the heavy shading by the evergreen frutescent layer, to the heavy stand of herbs, or to the heavy litter. In the subalpine spruce-fir formation *(Piceetum rubentis* and *Abietum Fraseri)* a ground layer of bryophytes, composing the *Hylocomium splendens* union, is characteristic, especially in the Abietum, and sometimes is complete. The fragmentary stands under the hardwoods were not studied and attention was centered on the terrestrial communities of the spruce-fir formation.

Our first determination was that of the minimum quadrat area. This was caried out at the same time that the regular samples were taken by a procedure which would permit a decision as to whether larger or additional sample plots would be necessary. One sq. m. quadrats were laid out five meters apart. Within these 1 sq. m. quadrats the species list and the coverage class for each species were noted separately for subdivisions of 0.1, 0.25, 0.5 sq. m. as well as for the entire quadrat. After making the four separate lists for the first set, we then progressed to the second set, etc. until an adequate number had been investigated.

For the *Piceetum rubentis* of Mt. Mingus 12 quadrat sets were employed. It happened that the series of 0.1 sq. m. samples encountered all the seven species which were revealed by the series of 1.0 sq. m. samples. With respect to the average number of species per quadrat for each of the series of different size, we found the following result, which is practically a straight-line relationship: for 0.1 sq. m. quadrats, 2.08 species; for 0.25 sq. m. quadrats, 2.25 species; for 0.5 sq. m. quadrats, 2.5 species; for 1.0 quadrats, 2.83 species. Since these data for the average number of species per quadrat, if plotted against the size of the quadrat, do not show a tendency to flatten out with increased quadrat size, one might conclude that a sample area larger than

1.0 sq. m. would be necessary. That would be true if only one sample per stand was taken, but on a basis of several samples from a stand we find that the 0.1 sq. m. quadrats reveal the same component species in the same quantitative relationships as do the 1.0 sq. m. samples. Therefore, the small sample areas are of adequate size if a sufficient number of them are examined. However, having obtained data for 12 quadrats of 1.0 sq. m. size, the results for that size are given in Table 6.

With respect to the number of quadrats necessary, the curves in Fig. 1

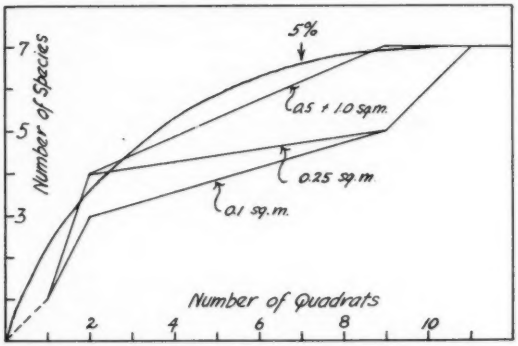

Fig. 1. Species-area curve for the *Hylocomium splendens* union of Piceetum rubentis based on 12 quadrats of 1.0 sq. m. each. The straight lines show the results for series of quadrats of different sizes. Minimum number of quadrats is about seven; ten are certainly adequate. The 5% point indicated on the curve means that a 10% increase in area yields only a 5% increase in species.

indicate that the 12 quadrats taken are sufficient since the species-area curves are flattened (saturated) at the eleventh quadrat for the two smaller sizes and at the ninth quadrat for the two larger sizes and at the ninth quadrat for the two larger sizes. It is to be expected that the larger sample areas would indicate more quickly the characteristic species content, and that fewer throws would be required. The advantage of 10 quadrats of 1.0 sq. m. over inequadrat of 10 sq. m. lies in the scattering of the sample over the population and in the obtaining of frequency data.

The *Hylocomium splendens* union of the *Abietum Fraseri* on Mt. LeConte was found to be slightly richer in species than that under the Piceetum, having a total flora, according to the quadrat study, of nine species. In this instance 15 quadrats of each of the four sizes were used, again scattered 5 m. apart. The result obtained was that the 0.1 sq. m. quadrats showed seven of the nine species which were revealed by the 1.0 sq. m. quadrats. The 0.25 and 0.5 sq. m. quadrats sampled eight of the nine species. With respect to the average number of species per quadrat for each of the sets of different size, we find the following result: for 0.1 sq. m. quadrats, 2.8 species; for

0.25 sq. m. quadrats, 3.06 species; for 0.5 sq. m. quadrats, 3.26 species; for 1.0 sq. m. quadrats, 3.46 species.

With respect to the number of quadrats necessary for an adequate sample, the following curves, Fig. 2, indicate that the 15 quadrats taken are more than sufficient as the species-area curves become flat at the eighth quadrat. The data for the community are given in Table 1, based on the 1.0 sq. m. quadrats.

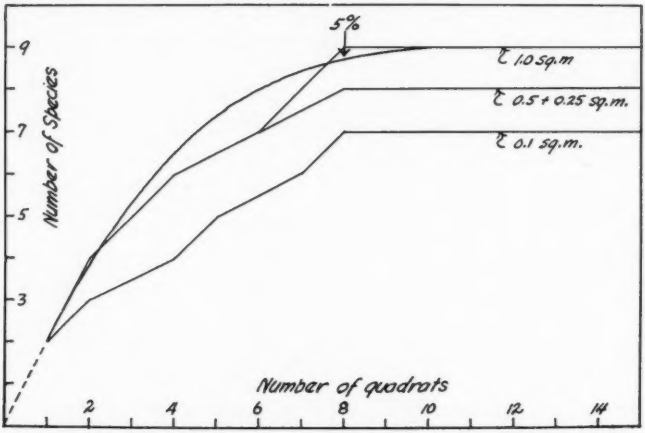

Fig. 2. Species-area curve for the *Hylocomium splendens* union of Abietum Fraseri. For a full explanation see the legend of figure 1.

B. Epilithic Communities

Bryophytic communities on rock under complete forest cover were studied by means of a series of 0.1 sq. m. quadrats (2 x 5 dm.). In the *Liriodendro-Tsugetum,* the *Halesio-Saccharodendretum,* and the *Aesculo-Tilietum,* these rock surfaces were of erratic conglomerate boulders of diverse sizes. Sometimes a single boulder supports more than one bryophytic community. In no case was a certain community sampled more than once from any one boulder. In these forest types the method used was to continue sampling all communities on successive boulders until the most frequent communities were encountered at least 10 times. For example, in the *Aesculo-Tilietum,* 27 boulders were examined, 10 of which supported unions of *Thuidium delicatulum* and *Hylocomium brevirostre.* Unions of *Dicranum fulvum* were found on only four boulders and of unions *Hedwigia ciliata* and *Mnium affine* var. *ciliare* were on two boulders each.

No comparable boulder communities were found in the Fagetum or the Piceetum in the localities studied. In the Abietum, however, the bryophytic unions on rock cliffs were examined. In numerous instances fragmentary communities of several different species were observed but not analyzed.

C. Epixylic Communities

These are the communities on trunks of fallen trees which have been down long enough to have lost completely their characteristic corticolous communities of the standing, living tree and to have developed the bryophytes typical of wood. The first series of these studies was made in the *Liriodendro-Tsugetum,* prinicipally on large hemlock logs. Here the procedure was to map the communities of a belt 1 m. wide, around the log, Fig. 3, giving the

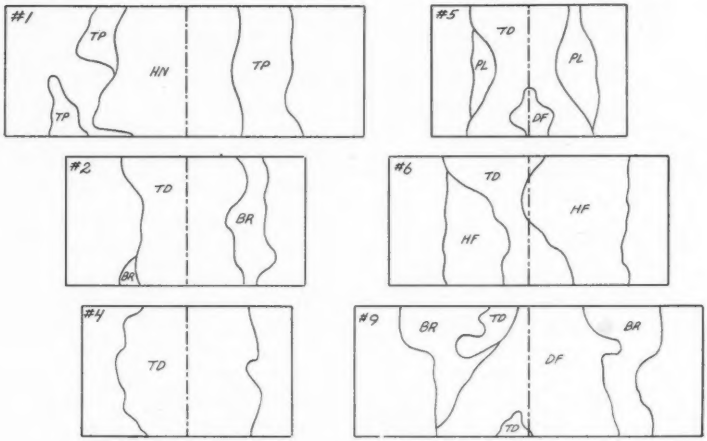

Fig. 3. Maps of the bryophytic communities of 1 m. wide belts around logs in the Liriodendro-Tsugetum. Nog No. 4 is red maple, No. 5 birch, and the rest hemlock. The communities indicated by initials are as follows: Hypnum union consisting of (HN) *Heterophyllum nemorosum* facies, (BR) *Brotherella recurvans* facies, (HF) *Hypnum fertile* facies; (TP) *Tetraphis pellucida* union; (TD) *Thuidium delicatulum* union; (PL) *Plagiothecium micans* union; (DF) *Dicranum fulvum* union.

coverage for each species in each community. In this manner 10 logs were studied. In studying logs of subsequent forest types it was decided that it was adequate and just as illuminating to use the method adopted for rock communities. Subsequently, each bryophytic community on a log was sampled by means of a 0.1 sq. m. quadrat (2 x 5 dm.).

D. Corticolous Communities

Bryophytic communities on living trees were studied in two ways. Lists of the characteristic top-limb flora were prepared by examination of obviously recently fallen branches. On this basis no quantitative data were obtained. Primary attention was paid to the tree butt flora which was mapped in all cases to at least 1 m. above the highest soil line (to a height of 2 m. for Fagus). Since many of the trees were quite large and stood on steep slopes,

the heigh of the mapped region was frequently close to 2 m. on the downhill side. Large roots extending above the general soil surface were also mapped. Each map shows the entire lower bark surface. The trunk was considered as a cylinder (truncated cone) split on the south side, unrolled and flattened out, Fig. 4. The cardinal points of the compass were marked at the height mentioned and the configuration of the tree-butt was sketched on cross-

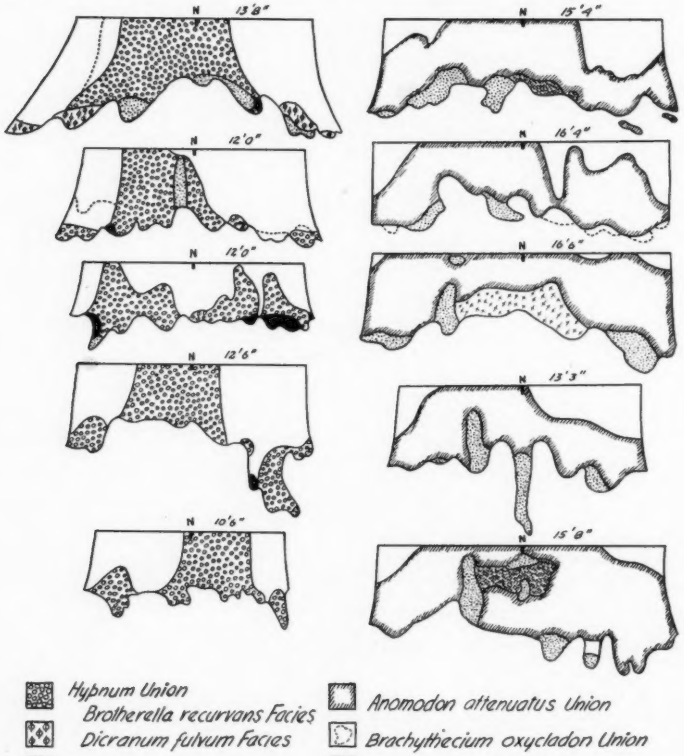

Fig. 4. Maps of the bryophytic communities on tree-butts. The five trees represented in the left-hand column are hemlock, principally with *Brotherella recurvans* facies of the Hypnum union. The five trees on the right are yellow poplar, principally with the *Anomodon attenuatus* union. Each map represents the tree-butt as if it was a cylinder split on the south and unrolled. The least height of the map in each case is one meter.

section paper. Careful measurements were made by means of a tape and meter stick. On this outline of the tree-butt the limits of the bryophytic communities were sketched in to scale except for areas where the total coverage of all species was less than 50 per cent. These areas were considered fragmentary stands, for the types of communities under consideration, and were ignored. Stands of higher cover were nearly always readily available.

In each forest type only the dominant tree species were studied. Three of the forest types were dominated by a single species only *(Piceetum rubentis, Abietum Fraseri, Fagetum grandifoliae subalpinum)*. Three other types studied were dominated by two species each *(Liriodendro-Tsugetum, Halesio-Saccharodendretum, Aesculo-Tilietum)*. In each instance 5 trees of each species were considered, making a total of 45 tree-butts which were mapped. The comparative data obtained on the different trees of the same species are interpreted as presence rather than constance because the areas of the individual stands vary from tree to tree.

E. Statistical Classes

The coverage classes used are divided as follows:

Class 5, covering 75-100 per cent of the area of the community
Class 4, covering 50-75 per cent of the area of the community
Class 3, covering 25-50 per cent of the area of the community
Class 2, covering 5-25 per cent of the area of the community
Class 1, covering 1-5 per cent of the area of the community
Class x, covering -1 per cent of the area of the community

The five frequency classes are each composed of 20 per cent, with class A, 1-20 per cent; class B, 20-40 per cent, etc. Presence and constance classes are likewise limited to 20 per cent each. These three terms are distinguished as follows: *frequence* per cent of a species is based on its occurrence in the several samples taken in one stand; both presence and constance are based on only one sample per stand. When the entire stand is taken as a sample the occurrence of a species in a certain number of the stands is termed *presence*. Quite naturally the different stands are of different sizes and the larger stands of a community may be expected, on the average, to contain more species. (To constitute a sample, a stand must be of minimal area, i.e. of sufficient size to permit the development of the combination of species which is characteristic for the particular community type.) When only one sample per stand is taken, always using a quadrat of uniform size, the percentage occurrence of a species is termed *constance*.

IV. Results

A. Bryophytic Communities of the Subalpine Forest Types

The subalpine forest types here treated include the following associations: *Abietum Fraseri, Piceetum rubentis,* and *Fagetum grandifoliae subalpinum*. The first two associations were described by Cain (1935). The bryophytic communities here investigated occur at the same stations studied previously.

1. Abietum Fraseri (Southern Balsam Fir Association)

In the spruce-fir formation of the Great Smoky Mountains *Abies Fraseri* is increasingly abundant the higher the elevation. On poorer sites around 6,000 ft. elevelation or above the fir frequently is dominant. At the station on Mt. LeConte, 6,500 ft. elevation, we find the following composition, based on 50 quadrats of 50 sq. m. each (Cain 1935).

Abies Fraseri	161.43 sq. ft. basal area,	90.7%
Picea rubens,	7.58 sq. ft. basal area,	4.2%
Sorbus americana	5.32 sq. ft. basal area,	2.9%
Betula allegheniensis	2.38 sq. ft. basal area,	1.9%
Prunus pennsylvanica	1.26 sq. ft. basal area,	.7%
Total	177.97 sq. ft. basal area	

The trees average about 50 ft. in height. The basal area is 288 sq. ft. per acre.

The frutescent layer has a coverage of class 2 and an average height of about 6 ft. The herbaceous layer has an average cover of class 3. The bryophytic soil layer has an average cover of class 5 except locally where the herbs or shrubs are excessively dense.

a. *Terrestrial communities: Hylocomium splendens* Union

The results of this investigation, based on 15 quadrats each of 1 sq. m., are given in Table 1. The whole area sampled is considered as one stand and the results are expressed by coverage classes and frequency for each species. The figures and symbols in the table indicate the occurrence of a species in a quadrat and stand for the coverage class (sometimes referred to as dominance class). The soil layer under Abies Fraseri in this typical locality is definitely referable to a single bryophytic community, the *Hylo-*

Table 1

Hylocomium splendens union on soil under Abietum Fraseri

Component species	Quadrats and coverage classes															Frequency
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Hylocomium splendens	**5**	**4**	**5**	**4**	**5**	**5**	2	**3**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	5
Rhytidiadelphus triquetrus	x	2	1	x	x	x	**3**	**3**		2	x	x	2		x	4
Hylocomium umbratum		x			x			2	x	x		1	x		x	3
Dicranum fuscescens		x														1
Hypnum crista-castrensis			x		x	x	2		1	x		x	x		x	4
Polytrichum ohioense				2											1	1
Thuidium delicatulum						x										1
Cephalozia bicuspidata								x	x							1
Plagiothecium laetum								x								1
Number of species	2	4	3	3	4	4	3	5	4	4	2	4	4	1	5	
Total coverage per cent	95	80	100	80	90	95	80	95	95	100	100	100	100	95	95	

comium splendens union. That species not only has the highest frequence but is consistently of high coverage, averaging class 5. Three other species have a fairly high frequence and occasionally have a class 2 or 3 coverage, namely *Hypnum Crista-castrensis, Rhytidiadelphus triquetrus,* and *Hylocomium umbratum.* The total bryophytic coverage for each quadrat was estimated to the nearest 5 per cent and never falls below 80 per cent on the quadrats. The total flora sampled includes eight mosses and one liverwort. The average number of species per sq. m. is only 3.5. Additional terrestrial species, not sampled by the quadrats, include *Calliergonella Schreberi, Hylocomium brevirostre, Dicranella heteromalla, Pohlia elongata, Bazzania trilobata,* and *Lepidozia reptans.*

Nine of the 15 quadrats contained small seedlings of *Abies Fraseri.* All quadrats contained numerous plants of *Oxalis montana* and some plants of either *Dryopteris dilatata* or *Athyrium angustum.* About one-fifth of the quadrats contained plants of *Aster acuminatus* and *Solidago glomerata.*

b. *Epilithic communities: Polytrichum ohioense* union : *Sphagnum* union

The bryophytic communities of the rock surfaces which were studied are confined to cliff faces. All the smaller eratic boulders lying close to the soil are overgrown by some bryophytic and herbaceous vegetation that covers the soil. The larger boulder and cliff ledges bear a similar flora, and in addition shrubs and trees. Consequently only the rock cliffs were studied for typically epilithic communities. From Table 2 it will be noted that even here the flora

TABLE 2

Polytrichum ohioense and Sphagnum unions on rock cliffs under Abietum Fraseri: 0.1 sq. m. quadrats, 10 stands.

	Polytrichum union					Sphagnum union				
	1	2	4	8	10	3	5	6	7	9
Common species										
Polytrichum ohioense	5	5	5	5	5	2	1	x	1	
Sphagnum spp.	1	1				4	5	5	5	5
Scapania nemorosa	1		1	x		1	x	x		
Hylocomium splendens	x				2		1	x	1	1
Dicranodontium denudatum			1	x		1	1			
Bazzania trilobata	1									
Cephalozia media			x							
Lophozia incisa			x							
Differential species										
Bazzania tricrenata				1						
Pohlia elongata				1						
Lepidozia reptans						x				
Dicranum fuscescens							x			
Hylocomium umbratum							x			x
Jamesoniella autumnalis								x		
Cephalozia bicuspidata								x		x
Herberta tenuis								x		
Number of species	5	2	5	5	2	5	7	7	3	4
Total coverage per cent	95	100	100	100	100	95	90	100	100	100

TABLE 3

*Cephalozia curvifolia, Dicranum fuscescens, Hylocomium splendens, and Sphenolobus Michauxii unions on 19 logs under Abietum Fraseri: 0.1 sq. m. quadrats.

	Cephalozia union					Dicranum union					Hylocomium union					Sphenolobus union				
	1	5	11	13	14	2	4	7	8	10	3	6	8	9	12	15	16	17	18	19
Dominant species																				
*Cephalozia curvifolia	5	**5**	**4**	**5**	**5**		2											2	2	1
Dicranum fuscescens		x				**4**	**4**	**5**	**4**	**5**						2			2	x
Hylocomium splendens											**5**	**5**	**4**	**5**	**4**					
*Sphenolobus Michauxii	1	1			x	x	1									**5**	**5**	**4**	**4**	**4**
Associated species																				
Brotherella recurvans					1	**3**	2	1	**3**	1		x						x	x	
Polytrichum ohicense											1		**3**		1					
Hypnum Crista-castrensis						x						2			**3**					
Geocalyx graveolens						x											2		1	
Lepidozia reptans		x	x	x		x	1									x	1		x	
Jamesoniella autumnalis							x	x										x	x	
Cephalozia ambigua					x		1													
Dicranum scoparium							x													
Hylocomium umbratum										x	x		x	x						
Thuidium delicatulum										x										
Calypogeia suecica				x	x															
Cephalozia media				x							x									
Riccardia palmata					x															
Blepharostoma trichophyllum											x									
Rhytidiadelphus triquetrus												x	x	x						
Scapania nemorosa																1	1			
*Sphenolobus exsectus																x	1	1	x	2
Lophozia incisa																				x
Number of species	2	4	2	4	5	6	8	3	2	4	5	4	4	3	3	5	5	5	8	5
Total coverage per cent	90	85	70	90	90	95	85	100	100	100	100	100	100	100	100	100	100	80	95	85

* An asterisk preceding a name indicates a synonym (to be found on pg. 252) resulting from the new check list by Buch, Evans and Verdoorn appearing after this paper was in type.

is in large part not truly epilithic but to a considerable extent is composed of species requiring some accumulation of soil. These species get started in small pockets and crevices in the rock, even on vertical faces and, due to the high humidity which exists most of the time, grow luxuriantly forming extensive mats over the surface, sometimes hanging free from the rock.

The two unions recognized in this habitat are obviously distinct despite the fact that they have five species in common. Each union has a single conspicuous dominant and also six exclusive species. The species of *Sphagnum* found in the plots were not determined in the field but the following three species had been collected previously from the same locality by Mr. Sharp and determined by Professor A. LeRoy Andrews: *Sphagnum squarrosum, S. Girgensohnii,* and *S. imbricatum* var. *affine.* Fragmentary unions are formed by *Dicranodontium denudatum, Herberta tenuis,* and *Scapania nemorosa.* Two additional species frequent in the area were not encountered in the quadrats: *Scapania undulata* and *Dicranum fulvum.*

c. *Epixylic communities:* **Cephalozia curvifolia* union
: *Sphenolobus Michauxii* union
: *Dicranum fuscescens* union
: *Hylocomium splendens* union

The nineteen logs which were sampled bore the four typical unions listed above, and in Table 3. Three of the unions have a definite successional relationship. The **Cephalozia curvifolia* union appears first, that is, on the more recently fallen logs. (It should be explained that it is characteristic for the pole stands of *Abies Fraseri* to have a large number of standing trees which are dead. The trees are all relatively small and crowded. Many trees are killed by shading and root competition in the rocky soil but do not soon fall down because of their interlacing branches and roots. Nearly always a tree stands a few years after dying and loses its bark and the majority of its limbs. Consequently, when it falls to the ground it is already a bare pole and partially decayed—a ready habitat for certain bryophytes.) The *Cephalozia* union is followed by the *Dicranum fuscescens* union and it in turn by the *Hylocomium splendens* union, which is characteristic of soil. There is little difference between the cover of a badly decayed log and that of the soil. Five of the eight species of the *Hylocomium union* on logs belong to the same association on soil. The three species which are not found also on soil occured only on one log apiece.

Seven of the nine species of the **Cephalozia curvifolia* union are liverworts. In the intermediate stage of the succession, the *Dicranum* union, half of the 12 species are liverworts. In the ultimate stage on logs, the *Hylocomium* union, only two of the eight species are liverworts. There is then a very distinct successional relationship between liverworts and mosses. The **Sphenolobus Michauxii* union is distinctly comparable with the *Cephalozia curvifolia* union. It was found on a series of logs lying on a steep north-facing slope. It is evident that water frequently trickles down these logs, both directly from rain and from seepage onto the upper ends. In this union eight of the

appearing after this paper was in type.

10 species are liverworts. The two mosses are common to both unions; three of the liverworts are held in common; four are distinct for the **Cephalozia* union, and five are distinct for the **Sphenolobus* union. The latter community is undoubtedly succeeded eventually by the *Hylocomium* union. Although transitional stages were not observed, other logs in the same relative position are occupied by the *Hylocomium* union. Occasionally almost pure colonies of relatively small size were found on the logs; they were dominated by *Bazzania trilobata, Geocalyx graveolens,* or *Hypnum crista-castrensis.* These were considered to be smaller than the necessary minimum-area for the development of typical community structure.

TABLE 4

Frullania Asagrayana, Hylocomium splendens, and the Hylocomium-Bazzania communities on tree-butts of Abies Fraseri mapped to 1 m. above the soil line.

	Frullania union					Hylocomium union						
						Typicum				Bazzania facies		
	1	2	3	4	5	2	3	4	5	2	3	5
Dominant species												
Frullania Asagrayana	2	3	2	3	3							
Hylocomium splendens					x	4	4	1	4	x	x	
Bazzania denudata		1	1		1		1		x	4	4	4
Associated species												
Herberta tenuis	3	3	2	1	2		x		x	2	1	
Brotherella recurvans	1	1	2	2	x	1	1	x	x	2	1	
**Sphenolobus exsectus*	1	1	x	1	1			x	x	1	x	2
Dicranum fuscescens	1	x	1	2		x	x				x	
Plagiochila tridenticulata	x	x	2		x							
Hypnum reptile	1	x	1	x	1							
Zygodon viridissimus	x	x	1	x	x							
Mylia cuneifolia	x	1	x	x								
Blepharostoma trichophyllum	x	1	1	x	x	x	x	x	x	1	1	x
Thuidium delicatulum			x	x	x	2	2	2	1	x	x	x
Polytrichum ohioense						x	1	4	2			
Hypnum Crista-castrensis						x	1		x			
Lepidozia reptans		x	x	x		x	x			1	1	
Geocalyx graveolens		x	x				x				x	
**Sphenolobus Michauxii*				x						x		
Bazzania nudicaulis	x	x	x	x	x							
Plagiothecium laetum	x		x	x	x		x	1	x	x	x	x
Paraleucobryum longifolium	x	x		x	x							
Lophozia incisa		x										
Jamesoniella autumnalis							x					
Microlejeunea ulicina				x								
Rhytidiadelphus triquetrus					x				x			
Leptodontium excelsum			x									
Tetraphis pellucida										x	x	
Cephalozia media										x	x	x
Hylocomium umbratum										x		
Number of species	13	16	17	16	15	8	13	7	11	13	13	6
Total coverage per cent	80	90	75	85	65	80	90	90	95	90	90	90

d. *Corticolous communities: Frullania Asagrayana* union
: *Hylocomium splendens* union
: *Hylocomium-Bazzania denudata* facies

The trunks of five trees of *Abies Fraseri* were mapped to a height of 1 m. above the highest soil line and found to be covered principally by a union of *Frullania Asagrayana*. Two other unions the *Hylocomium splendens* union, and a facies of that community, *Hylocomium-Bazzania denudata* facies, occurred on the lower parts of the trunks and on the short exposed roots, Table 4. The second meter above the ground was also occupied by the *Frullania* union with essentially the same component species. Above that height it was impossible to make accurate observations from the ground but it appeared that the same community extended upward a considerable distance essentially unchanged except for reduced total coverage.

The *Frullania* union is exceedingly rich in species, totaling 22, and is uniform as to composition on the different trees. Thirteen of the species are liverworts and nine are mosses. It is not a strongly dominated community but the total coverage of *Frullania Asagrayana* is greater than that of *Herberta tenuis*—a fact which is not so obvious when only coverage classes are recorded (Table 4). Also, *Frullania* is the more characteristic species of the community over a much wide range of trees and forest types.

The *Hylocomium splendens* union is similar to that on logs and soil but different species occur, as would be expected from the nature of the habitat. The facies of that union, dominated by *Bazzania denudata,* is obviously closely related to the *Hylocomium* union as 11 of the 15 species are held in common. Each community has four species which are distinctive. It is also quite to be expected that the *Hylocomium* and the *Frullania* unions would have several species in common. There are in fact 11 species of the former which occur in the latter. The communities are distinct, however, especially as to dominants. The *Hylocomium* union and its facies have an important dependence on proximity to the soil and are to be considered as only partially corticolous.

The top-limb flora includes the following bryophytic species in addition to the abundant lichens which were not studied: *Frullania Asagrayana, Ulota crispa, Paraleucobryum longifolium, Hypnum reptile, Leptodontium excelsum,* and *Zygodon viridissimus.*

The eight bryophytic unions of the *Abietum Fraseri* of Mt. LeConte are summarized in Table 5.

2. Piceetum rubentis (Red Spruce Association)

In the spruce-fir formation of the Great Smoky Mountains *Picea rubens* is dominant on the better sites, especially at lower elevations. Magnificent spruce forests are found at elevations of 5,000 to 5,500 ft. The present study is based on a stand at 5,000 ft. on Mt. Mingus, described by Cain (1935). There we find the following tree composition, based on 50 quadrats of 200 sq. m. each (10 x 20 m.).

Picea rubens	727.95 sq. ft. basal area,	88.9%
Abies Fraseri	60.37 sq. ft. basal area,	7.3
Betula allegheniensis	20.41 sq. ft. basal arear,	2.5
Amelanchier laevis	3.49	
Ilex monticola	2.06	
Fagus grandifolia	1.75	
Sorbus americana	1.17	2.3
Acer spicatum	.47	
Acer pennsylvanicum	.19	
Total	818.40 sq. ft. basal area	

The trees average about 120 ft. high with a basal area of 327 sq. ft. per acre.

TABLE 5

Summary of the bryophytic communities of Abietum Fraseri.

Unions of	Substratum			
	Terrestrial	Epilithic	Epixylic	Corticolous
Hylocomium splendens	X	--	X	X
Hylocomium-Bazzania denudata facies	--	--	--	X
Polytrichum ohioense	--	X	--	--
Sphagnum spp.	--	X	--	--
**Cephalozia curvifolia*	--	--	X	--
**Sphenolobus Michauxii*	--	--	X	--
Dicranum fuscescens	--	--	X	--
Frullania Asagrayana	--	--	--	X

The frutescent layer has a coverage of class 2 and an average height of about 6 ft.; the herbaceous layer has an average cover of class 2 and the bryophytic layer a cover of class 4. Both the latter layers cover less than they do in the more humid Abietum.

a. *Terrestrial communities: Hylocomium splendens* union

The results of this investigation are given in Table 6, based on 12 quadrats of 1 sq. m. each. The whole area sampled is considered as one stand,

TABLE 6

Hylocomium splendens union on soil under Piceetum rubentis, based on twelve 1 sq. m. quadrats.

Component species	Quadrats and coverage classes												Frequency
	1	2	3	4	5	6	7	8	9	10	11	12	
Hyclomium splendens	**5**	**4**	**5**	**5**	**5**	**4**	**5**	**5**	**3**	**5**	**4**	**5**	5
Hypnum Crista-castrensis		x	x	x	1	x	x	1	1	x	x	x	5
Dicranum scoparium		x			x						x		2
Polytrichum ohioense		x											1
Brotherella recurvans									x	x	2		2
Dicranum fuscescens									x		x		1
Bazzania trilobata									x		x		1
Number of species	1	4	2	2	3	2	2	2	5	3	6	2	
Total coverage per cent	100	70	95	95	100	70	95	95	50	95	80	100	

consequently the figures in the right-hand column of the table represent frequency classes. The other figures and symbols represent coverage classes for each species in each quadrat. The soil layer is quite definitely assignable to the same community as that under Abietum, namely, the *Hylocomium splendens* union. Although *Rhytidiadelphus triquetris*, a species of class 4 frequency under Abies, is absent here and three of the seven species under Picea are not found under Abies, we nevertheless find *Hypnum Cristacastrensis* and *Hylocomium splendens* again to be of high frequency and the latter of high coverage. This flora includes only one liverwort, *Bazzania trilobata*, of sporadic occurrence and low coverage. There are very few herbs in this portion of the forest. The soil, herb, and shrub layers more or less alternate, forming a mosaic according to the balance between slope, shade, and soil conditions.

b. *Epilithic communities*

The slopes on which this phytocoenosis stands are essentially free of erratic boulders and cliffs, consequently no study was made of the very scattered and fragmentary communities which were seen.

c. *Epixylic communities: *Cephalozia curvifolia* union
: *Dicranum fuscescens* union
: *Brotherella recurvans* facies

Fourteen logs were sampled by 0.1 sq. m. quadrats revealing the three typical epixylic communities listed above, and in Table 7. The **Cephalozia curvifolia* and *Dicranum fuscescens* unions again accur as they did under *Abies*, with the former developing first and gradually being replaced by the *Dicranum* union. This in turn is succeeded by the *Brotherella* facies. The most conspicuous contrast between the log communities under *Abies* and under *Picea* is the absence of the final dominant, the *Hylocomium splendens* union, on logs under *Picea*. There certainly is no question as to its availability, since it is dominant on soil under *Picea*. The explanation would seem to lie in the lesser, although still high, humidity of the Piceetum as compared with the Abietum.

Although the *Dicranum* union is in places dominated by *D. scoparium* it is nevertheless better considered merely as an aspect of the *Dicranum fuscescens* union.

d. *Corticolous communities: Frullania Asagrayana* union
: *Hypnum-Bazzania trilobata* facies
: *Brotherella recurvans* facies

The trunks of five large trees of *Picea rubens* were mapped to a height of 1 m. above the highest soil line. These trees contrast in several ways with the fir trees described earlier. In the first place, the more rapid flaking-off of the bark on the main part of the trunk does not allow time for the extensive development of closed communities. A 50 per cent cover, arbitrarily taken as the least coverage limit for our community mapping and samples, is

TABLE 7

*Cephalozia curvifolia, Dicranum fuscescens, and Brotherella recurvans communities on logs under Piceetum rubentis on Mt. Mingus, based on 0.1 sq. m. quadrats from 14 logs.

	Brotherella facies						Dicranum union					*Cephalozia union					
	1	2	4	6	7	9	2	8	9	10	13	3	4	9	11	12	14
Dominant species																	
Brotherella recurvens ____	**4**	**4**	**5**	**5**	x	**5**	2	2	2	x							
Dicranum fuscescens ____	1	2	x	1	x	x	4	4	x	2							
Dicranum scoparium ____						1			4	4	4						
**Cephalozia curvifolia* ____	1	x						x				4	4	4	4	4	5
Associate species																	
Hypnum reptile _____	2				4												
Bazzania trilobata _____	x	x	x				x	1			3	x					
**Sphenolobus Michauxii* __	x				2												
Frullania Asagrayana ____	x				x												
*Hypnum Crista-castrensis*__	x		x	1													
Hypnum fertile _____	x	x		x		x				2				x			x
Lepidozia reptans _____		x	1		x		x	x									
*Heterophyllum nemorosum*_			x			x			x								
Herberta tenuis _____					x												
**Sphenolobus exsectus* ____					x												
Thuidium delicatulum ____							x										
Paraleucobryum longifolium							x										
Cephalozia media _____								x									
Colliergonella Schreberi __									x								
Hylocomium splendens ___									x	x							
Hypnum imponens _____											1						
Jamesoniella autumnalis __															x		x
Riccardia palmata _____																2	
Number of species ____	9	6	6	4	8	5	6	6	6	5	3	2	1	2	2	2	3
Total coverage per cent__	95	70	100	95	100	100	90	90	100	95	100	70	55	55	55	80	90

seldom found except on the roots and in the sinuses of the lower part of the trunks. The flakes of bark have mainly *Frullania Asagrayana* and *Hypnum reptile* on them when they fall from the trunk. Only one trunk showed a stand of *Frullania* exceeding 50 per cent. This was on the south side of tree no. 3. The exposed roots and sinuses of the trunk support two unions. The *Hypnum-Bazzania trilobata* facies is the more extensive community and extends higher up the trunk—to 1 m. or more. The *Brotherella recurvans* facies is more frequently found on roots although it too may extend up sinuses to a height of 1 m., Table 8.

In comparison with communities on *Abies*, those on *Picea* are much impoverished. The total flora is 16 as opposed to 29 species on *Abies*. The *Frullania* union has only 4 species in comparison with 22 species on *Abies*. The *Hypnum-Bazzania trilobata* and *Brotherella recurvans* facies are equally rich as the corticolous *Hylocomium* union of *Abies*. *Hypnum fertile* is the only moss of the *Frullania union*. About half the flora of the two other communities is made up of liverworts. The communities lower on the trunk

undoubtedly bear relations with the soil proximity (more dust, greater humidity, etc.) and with water seepage down the trunk sinuses.

The top-limb flora is similar to that of *Abies*.

The six bryophytic communities of the *Piceetum rubentis* of Mt. Mingus are summarized in Table 9.

TABLE 8

Frullania Asagrayana, Brotherella recurvans, and Hypnum-Bazzania trilobata communities on tree-butts of Picea rubens mapped to a height of 1 m. above the soil, Mt. Mingus.

	Hypnum union									Frullania union	
	Bazzania trilobata facies					Brotherella recurvans facies					
	1	2	3	4	5	1	2	3	4	5	3
Dominan species											
Bazzania trilobata	**5**	**3**	**5**	**5**	**4**	2	2	1	1		
Hypnum fertile	1	x	x		1	**3**	2	**3**	2		1
Frullania Asagrayana		x						x			**3**
Brotherella recurvans		2	x	x	1	**3**	**3**	2	**3**	**4**	
Associated species											
Bazzania nudicaulis	1										
Baazzania denudata					x						
Dicranum fuscescens	x	x	1		1	x	1	1	1		
Hypnum reptile		1			x	x					
Lepidozia reptans		x			x	1		x	1		
Herberta tenuis		x			x	x		x	x		x
Tetraphis pellucida		x	x	x	x	x					
Thuidium delicatulum		x					2				
Hylocomium splendens			x			x	x		x		
**Cephalozia curvifolia*					x		x		x		2
Hypnum Crista-castrensis						x					
Blepharostoma trichophyllum								x			
Number of species	4	10	6	3	10	10	7	8	8	1	4
Total coverage per cent	90	55	95	80	80	60	90	60	60	60	55

TABLE 9

Summary of the bryophytic communities of Piceetum rubentis.

Unions of	Substratum			
	Terrestrial	Epilithic	Epixylic	Corticolous
Hylocomium splendens	X	--	--	--
**Cephalozia curvifolia*	--	--	X	--
Dicranum fuscescens	--	--	X	--
Brotherella recurvans facies	--	--	X	X
Frullania Asagrayana	--	--	--	X
Hypnum-Bazzania trilobata facies	--	--	--	X

3. Fagetum grandifoliae subalpinum (Beech gap association)

Although the beech is not a member of the spruce-fir forest formation it extends upward into the subalpine region where it is found in gaps and sometimes on saddle-like ridges at elevations as great as 5,500 ft. The spruce on favorable slopes may extend down to 4,500 ft. or less as a closed community with scattered trees a few hundred feet lower. There is then a considerable interlocking or alteration of conifer and hardwood communities.

The present study of bryophytic communities of the beech-gap forest type was made on a stand at Trillium Gap (until recently known as Beech Gap or Grassy Gap) at an elevation of 4,700 ft. The Gap lies between Brushy Mt. and a lead southward to Mt. LeConte, almost 2,000 ft. higher. The beech community occupies a few acres in the gap and soon gives way to spruce on the ridge leading to LeConte, and to the peculiar frutescent "heathbald" type of vegetation on Brushy Mt. The valleys leading from the saddle soon become occupied by "cove hardwoods"; a few hundred feet lower developing a codominance with *Tsuga canadensis*.

The subalpine beech forest type is dominated by *Fagus grandifolia* which usually composes 90 percent or more of the stand. Associated species include *Aesculus octandra, Betula allegheniensis, Ilex monticola, Halesia monticola,* and occasionally others, either from the cove hardwoods or from the spruce forest. The trees of the beech gap forest type are very poorly developed. Frequently they average only 20-30 ft. in height and are poorly formed and broken. The soil of this woods never shows any peat accumulation or podzolization as do the soils of the contiguous vegetation types, nor is there any layer of evergreen shrubs as *Rhododendron* spp. and *Kalmia latifolia*.

The hydrogen-ion concentration of the soil averages around pH 5.0, much less acid than that of the soils of contiguous forest types.

The beech may be a distinct ecospecies, as it is usually more or less disjunct from other beech trees by a few hundred feet of elevation. In fact, good development of beech usually occurs at elevations of 3,500 ft. or lower where it is a member of the cove hardwoods. The characteristic occurrence of Fagetum grandifoliae subalpinum in gaps from 4,500 to 5,500 ft. elevation is probably attributable to wind movements and the concommitant fogs, frosts, and sleets. The taxonomic and ecologic status of this beech has not yet been investigated thoroughly.

a. *Terrestrial communities:*

Soil mosses are conspicuously absent. This situation is attributed to the heavy stand of herbs. In places tall grasses and sedges form a fairly heavy sod to which is added such large and conspicuous fllowering herbs as *Eupatorium urticaefolium, Rudbeckia laciniata,* and *Solidago Curtisii*.

b. *Epilithic communities*:

Large erratic boulders and cliffs are usually absent from the gaps although here and there, on small stones, one sees fragmentary communities of *Hylocomium brevirostre, Thuidium delicatulum,* or *Dicranum fulvum*.

c. *Epixylic communities:*

Since the trees are small, such logs as one finds are usually so heavily shaded that they possess no well-developed bryophytic flora. Fragmentary epixylic communities were observed which were dominated by *Hypnum imponens, H. fertile, Thuidium delicatulum,* or *Mnium affine* var. *ciliare.*

d. *Corticolous communities: Ulota-Leucodon brachypus* facies
: *Ulota americana* facies
: *Neckera pennata* union
: *Anomodon Rugelii* facies
: *Dicranum fulvum* union

Epiphytic communities of bryophytes and lichens are exceptionally well-developed in this forest type. From the soil-line to the periphery of the crown the coverage is almost complete. Five trunks of beech were mapped to a height of 2 m. above the soil-line and found to support a total of five communities of bryophytes, usually about two kinds of communities to a tree, Table 10.

TABLE 10

Ulota-Leucodon brachypus, Ulota americana, Neckera pennata, Anomodon Rugelii, Dicranum fulvum communities on Fagus grandifolia at Trillium Gap, 4,700 ft. elevation.

	Ulota-Leucodon brachypus facies			Anomodon facies		Ulota americana facies				Di-cranum union	Neck-era union
	1	2	3	3	5	1	2	3	4	4	5
Dominant species											
Leucodon brachypus	4	**3**	**3**	x	2	x	1	x	x	x	x
Anomodon Rugelii	x	x		**3**	**4**	1	x	x	x		1
Ulota americana var. *rufescens*	1	2	**3**	x	x	2	**3**	**3**	**3**	1	
Dicranum fulvum		x	1	x			x	x	1	**5**	
Neckera pennata					x						**4**
Associated species											
Anomodon tristis	x	x	1	x	2	2	x	x			2
Schwetschkeopsis denticulata	x	1	1	2	x	1	2	x			x
Ulota crispa	x	x	x			x	1		2	x	
Frullania eboracensis	1	1	x			1	1		1	x	
Porella platyphylloidea	x	2		x	x	1	x		x		x
Homalotheciella subcapillata	x	1	x			1	x				
Homomallium adnatum	x		x	x	x	2		2			x
Dicranum scoparium						x					
Radula caloosiensis		x	x	x	x		x				
Metzgeria crassipilis							x				
Orthotrichum pumilum			x		x						x
Entodon brevisetus			x	x	x						
Brachythecium oxycladon									x		
Metzgeria furcata					x						
Cololejeunea Biddlecomiae					x						
Number of species	10	11	12	10	13	11	11	7	8	5	8
Total coverage per cent	80	90	90	90	85	70	80	70	75	95	95

The *Ulota-Leucodon brachypus* facies usually extends from about 0.5 to 1.0 m. above the soil upward to well above the 2 m. limit of the maps. The *Neckera pennata* union is comparable to the preceding. The *Ulota americana* facies usually occupies the lower part of the trunk but may extend upward to a considerable height if the competition with the larger (pleurocarpous) mosses is not too great. The *Anomodon Rugelii* facies is found in the lower sinuses of the trunk or may, on some trees, cover most of the trunk to a height of more than 2 m. The *Dicranum fulvum* union is usually seen in the sinuses of the trunk unoccupied by other associations. It develops a closed structure which cuts down the presence of other species.

These five communities are all closely related floristically but deserve recognition not only because of differences in dominance in the present forest type but also because of their distinctness elsewhere. None of these communities is found on the lower parts of trunks of spruce and fir as studied on Mt. Mingus and Mt. LeConte.

The top-limb flora is composed of the following species: *Ulota crispa, Leucodon brachypus, Orthotrichum pumilum, Anacamptodon splachnoides, Platygyrium repens, Drummondia prorepens* and the liverwort *Porella platyphylloidia.*

B. Bryophytic Communities of the Cove Hardwood Forest Types

A common broad interpretation of the primeval forest types of the Great Smoky Mountains National Park sets up three major divisions: the subalpine spruce-fir forest, the cove hardwoods, and the chestnut-oak-hickory-pine complex. A detailed sample-plot study of the cove hardwoods is in preparation by the senior author. This study includes among others the stations here used for bryocoenological investigation. Three forest associations belonging to the cove hardwoods have been selected for a study of their bryophytic communities: *Aesculo-Tilietum, Halesio-Saccharodendretum,* and *Liriodendro-Tsugetum.* The first and third of these types are well characterized floristically and ecologically. The second type is less well marked off. We can, in fact, make the general statement concerning the whole cove hardwoods complex, that it is characterized by a relative richness of species (for primeval vegetation), general optimum growing conditions, and gradual ecotonal transitions. Several tree species range rather widely with respect to altitude, topography (slope and exposure), and soil factors. The result is that the forest presents itself as a great mixture (at least for temperate montane conditions) in which chance may determine largely which species dominate locally. Considerable variations in floristic and percentile composition occur on what appear to be ecologically equivalent conditions. In the bryocoenological study no attempt has been made to define the bryophytic communities for any forestal phases other than those at the three locations named. These three stations are located in the Greenbrier region of the Park.

1. AESCULO-TILIETUM (Buckeye-Basswood Association)

This forest type was studied at 3,800 ft. elevation on Buck Fork, one of the tributaries of the Little Pigeon River in the Greenbrier region, which heads up on Mt. Guyot. Stands of this type are encountered in equivalent positions in nearly every valley of the region. A clearer picture of the location of this type can be obtained by a consideration of that orientation of the component forest types of the cove hardwoods complex which can be recognized. In the V-shaped valleys at lower elevations (the virgin forest usually is not found below 2,700-3,000 ft. elevation) one usually encounters, along the stream and covering the lower slopes, one or more forest types in which hemlock, *Tsuga canadensis*, is a codominant of varying importance with one or more of the following species: *Liriodendron tulipifera, Betula allegheniensis, Fagus grandifolia, Magnolia Fraseri, M. acuminata, Aesculus octandra, Tilia* spp., *Ilex opaca, Saccharodendron barbatum, Fraxinus americana, Halesia monticola,* etc. A conspicuous feature of the forests with hemlock in this location is the heavy understory of *Rhododendron maximum* and *Kalmia latifolia*. Very frequently the tree and shrub coverage is so high that it excludes all development of herbs and terrestrial bryophytes. If one leaves the bottom of the valley in such a region for the middle and upper slopes, drier forest types appear and one may encounter pure stands of hemlock (a ridge type) or members of the chestnut-oak-hickory-pine complex. If one travels up the valley to higher elevations the hemlock and rhododendron are left behind at elevations around 3,500 to 4,500 ft. The most characteristic forest type encountered at those altitudes in the valley bottom and lower slopes is the *Aesculo-Tilietum*. These stands may occupy only a few acres as a rather narow strip along the now quite small stream. As a consequence one finds a rank growth of herbs forming an almost complete carpet, not only on soil, but also over rocks and logs, and even on the tree-butts. The vernal aspect is marked by species of *Viola, Bicuculla (Dicentra), Claytonia, Panax, Anemone, Juncoides (Luzula), Poa, Phacelia, Erythronium, Trillium, Asarum (Hexastylis) Arisaema, Ranunculus,* etc. The aestival aspect is much taller with *Cimicifuga, Eupatorium, Solidago, Monarda, Blephilia, Aster, Urticastrum,* and several ferns, especially species of *Dryopteris* and *Athyrium*. The frutescent layer is quite fragmentary in most places. The structure of the forest type, at the present station, is given in Table 11.

TABLE 11

Composition of the tree layer, Aesculo-Tilietum, 3,800 ft. elevation on Buck Fork, Greenbrier. Total sample 4.200 sq. m.

Species	Basal area in sq. ft.	Per cent
Tilia neglecta	58.5	27.7
Aesculus octandra	59.7	28.3
Fagus grandifolia	35.2	16.7
Saccharodendron barbatum	34.9	16.5
Halesia monticola	11.6	5.5
Betula allegheniensis	6.6	2.2
Tsuga canadensis	4.1	2.2
	210.6	100.0

a. *Terrestrial communities:*

As a consequence of the above situation, with respect to the herb layer, to which must be added the fact that the terrain is usually strewn with large boulders, bryophytes have very little chance to develop terrestrial communities.

b. *Epilithic communities: Thuidium delicatulum* union
: *Hylocomium brevirostre* union
: *Dicranum fulvum* union
: *Hedwigia ciliata* union
: *Mnium affine* var. *ciliare* union

The abundant eratic boulders, covered with moss communities, were sampled by means of 0.1 sq. m. quadrats until a total of 27 boulders were examined. About two-thirds of them were covered with either the *Thuidium delicatulum* or the *Hylocomium brevirostre* unions. The other communities were encountered a relatively small number of times, Table 12. The two

TABLE 12

Thuidium delicatulum, Hylocomium brevirostre, Dicranum fulvum, Hedwigia ciliata, and Mnium affine ciliare unions on 27 rocks sampled by 0.1 sq. m. quadrats: Aesculo-Tilietum.

	Thuidium union									
	1	4	7	13	15	18	21	23	24	26
Thuidium delicatulum	**5**	**5**	**4**	**5**	**5**	**4**	**5**	**5**	**5**	**5**
Hylocomium brevirostre	x		2	x	1	2	x			x
Rhodobryum roseum	x									
Brachythecium oxycladon	x							x	1	
Dicranum fulvum					x		x			
Total coverage per cent	100	100	100	95	100	100	100	100	100	100

	Hylocomium union									
	5	6	7	8	10	11	12	14	17	22
Hylocomium brevirostre	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Thuidium delicatulum		1	x	x	x	1	1	1	x	1
Cirriphyllum piliferum						x				
Mnium affine var. *ciliare*						x				
Rhodobryum roseum							x			
Total coverage per cent	100	100	95	100	100	100	85	100	95	100

	Dicranum union				Hedwigia union		Mnium union	
	2	16	19	27	20	25	3	26
Dicranum fulvum	**5**	**4**	**4**	**5**		x		
Hedwigia ciliata		1	x	x	**5**	**4**		
Mnium affine var. *ciliare*							**5**	**5**
Thuidium delicatulum	x	x	x	x	x	x	x	x
Homomallium adnatum			x		1	2		
Brachythecium oxycladon				x				x
Ulota americana						x		
Hylocomium brevirostre							x	
Rhodobryum roseum								x
Total coverage per cent	100	75	75	90	95	80	95	95

principal communities of the tops and upper slopes of these conglomerate boulders are apparently ecologically equivalent. It would seem to be a matter of chance as to which dominates—probably which happens to colonize first. The three less frequent communities are more characteristic of the steeper sides of the boulders. Although these communities may occur on the tops of boulders they are quickly succeeded by the large pleurocarpous mosses. It will be noted that no liverworts occur in the communities.

Fragmentary communities were observed dominated by *Climacium americanum, Anomodon attenuatus, Brachythecium oxycladon,* and *Grimmia pilifera.*

c. *Epixylic communities: Thuidium delicatulum* union
: *Hypnum* union
Heterophyllum nemorosum facies
Hypnum imponens facies
Hypnum curvifolium facies
: *Anomodon Rugelii* facies
: *Mnium affine* var. *ciliare* union
: *Tetraphis pellucida* union
: *Hylocomium brevirostre* union

The communities on 20 logs under the *Aesculo-Tilietum* were sampled by 0.1 sq. m. quadrats, at which time the most frequent community, the *Thuidium delicatulum* union, was encountered 10 times, Table 13. We also found that unions dominated by species of *Hypnum* were encountered 11 times. These 11 communities of *Hypnum* are interpreted, however, as belonging to three facies: *Heterophyllum nemorosum, Hypnum imponens,* and *H. curvifolium* facies. In so far as our observations go, these three facies seem to be ecologically equivalent and it is a matter of mere chance which species occupies any particular log first and thus comes to dominate. The four remaining communities, although occurring infrequently on the logs examined,

TABLE 13

Epixylic communities of twenty logs under Aesculo-Tilietum sampled by 0.1 sq. m. quadrats.

	Thuidium union									
	1	4	5	7	8	10	15	18	19	20
Thuidium delicatulum	5	5	5	5	5	5	5	5	5	5
Mnium affine var. *ciliare*	x	x	x							
Rhodobryum roseum	x	x								
Hypnum curvifolium	x		x		x		x		x	
Neckera pennata	x									
Hylocomium brevirostre			x							
Hypnum fertile					x					
Dicranum scoparium					x	x	x	x		
Hypnum imponens						x	x	x		
Heterophyllum nemorosum							x	x		
Total coverage per cent	100	100	100	100	100	100	100	100	100	95

Hypnum union:	Heterophyllum nemorosum facies				Hypnum imponens facies				Hypnum curvifolium facies		
	14	16	17	18	3	9	10	13	1	7	12
Heterophyllum nemorosum	**5**	**5**	**5**	**5**	x	x	x				
Hypnum imponens		x		x	**5**	**5**	**5**	**5**			
Hypnum courvifolium					x				**5**	**5**	**5**
Thuidium delicatulum	x			x	x		x		x	x	
Hylocomium brevirostre	x										
Dicranum scoparium		x	x	x			x	x			
Dicranum fulvum				x							
Hypnum fertile										x	
Total coverage per cent	100	100	100	100	100	100	100	100	100	95	95

	Anomodon Rugelii facies		Mnium union		Tetraphis union		Hylocomium union
	1	6	2	6	10	16	11
Anomodon Rugelii	**5**	**5**					
Mnium affine var. *ciliare*			**5**	**4**			
Tetraphis pellucida					**5**	**5**	
Hylocomium brevirostre							**5**
Thuidium delicatulum	x	x	2	**3**			1
Brachythecium oxycladon	x	x	x				
Leucodon sp?	x						
Hypnum curvifolium	1						
Schwetschkeopsis denticulata		x					
Total coverage per cent	95	95	100	95	90	100	100

are perfectly regular and are encountered in many places within the cove forest complex.

Fragmentary communities of *Anomodon attenuatus, Brachythecium oxycladon,* or *Dicranum scoparium* were observed.

d. *Corticolous communities: Anomodon attenuatus* union
: *Anomodon Rugelii* facies
: *Thuidium delicatulum* union
: *Brachythecium oxycladon* union

Five trunks of *Aesculus octandra* and five trunks of *Tilia neglecta* were mapped to a height of 1 m. above the highest soil line. Little difference between the bryophytic communities on the bark of the two tree species was noticed, Table 14. Both were dominated in the main by *Anomodon attenuatus* with *A. rostratus* of second importance and with *A. Rugelii* in one instance with a coverage of class 5 and another with class 3. The *Thuidium* union in both cases occurred on roots near the soil as did the *Brachythecium* union. These latter communities are to be interpreted as not being strictly corticolous, but as depending to a considerable extent on humus accumulation.

Many phanerogams are found associated with the corticolous bryophytic communities, especially on *Aesculus,* up to a height of 2 m. above the ground. They do not, however, constitute a very great coverage. The species noted are as follows: *Sedum ternatum, Dentaria diphylla, Claytonia virginica, Poa cuspidata, Alsine (Stellaria) tennesseensis, Solidago caesia, Tiarella cordifolia,*

TABLE 14

Anomodon attenuatus, Anomodon Rugelii, Thuidium delicatulum, and Brachythecium oxycladon communities on tree-butts of Aesculus and Tilia mapped to a height of 1 m.

Communities on Aesculus octandra	Anomodon union					Brachythecium union		Thuidium union
	1	2	3	4	5	2	3	2
Anomodon attenuatus	**4**	**3**	**4**	**3**	**3**	x	**3**	x
Anomodon rostratus	2	**3**	**3**	**4**	**3**	x	x	
Anomodon Rugelii		x	1	**3**				
Brachythecium oxycladon	x	x	1	x	x	**5**	**4**	x
Thuidium delicatulum	x	x			x	x		**5**
Fissidens cristatus	x	x			x		1	
Neckera pennata	x		x		x			
Leptodon trichomitrion	x				x			
Frullania Asagrayana	x							
Campylium chrysophyllum	x							
Schwetschkeopsis denticulata	x							
Anomodon tristris	x							
Bryhnia novae-angliae	x							
Amblystegium serpens				x				
Leucodon sciuroides					x			
Homalotheciella subcapillata					x			
Thamnium allegheniense							x	
Rhodobryum roseum								x
Number of species	12	6	5	5	9	4	5	4
Total coverage per cent	70	80	85	95	65	80	90	95

Communities on Tilia	Anomodon union					Anomodon Rugelii facies	Thuidium union
	1	2	3	4	5	3	1
Anomodon attenuatus	**4**	**5**	**5**	**3**	**4**	x	x
Anomodon rostratus	2	x	2	**3**	2		
Anomodon Rugelii		x	x	x	x	**5**	
Thuidium delicatulum	x	x			x		**5**
Brachythecium oxycladon	x	x	x	x	x		x
Leptodon trichomitrion	x		x	x	x	x	
Neckera pennata	x		x		x	x	
Fissidens cristatus	x			x			x
Schwetschkeopsis denticulata		1					
Campylium chrysophyllum		x					
Radula caloosiensis		x					
Metzgeria conjugata		x					
Rhodobryum roseum			x				
Hylocomium brevirostre				x			
Leucodon sciuroides					x		
Homalotheciella subcapillata					x		
Number of species	7	9	7	7	9	4	4
Total coverage per cent	90	90	90	90	90	80	90

Monarda didyma, Bicuculla (Dicentra) canadensis, Rudbeckia laciniata, Phlox stolonifera, Viola canadensis, Cimicifuga americana, and *Viola blanda.* All smaller plants were able to flower and fruit in this situation.

The top-limb flora seems to be of low coverage (considering the region

as a whole) and to consist of a relatively small number of species. Those noted were *Ulota americana, U. crispa, Leucodon sciuroides, L. brachypus,* and *Frullania Asagrayana.*

The communities of this forest type are summarized in Table 15.

TABLE 15

Summary of the bryophytic communties of the Aesculo-Tilietum.

Unions of	Substratum				
				Corticolous	
	Terrestrial	Epilithic	Epixylic	Aesculus	Tilia
Thuidium delicatulum	--	X	X	X	X
Hylocomium brevirostre	--	X	X	--	--
Mnium affine var. *ciliare*	--	X	X	--	--
Dicranum fulvum	--	X	--	--	--
Hedwigia ciliata	--	X	--	--	--
Hypnum					
Heterophyllum nemorosum facies	--	--	X	--	--
Hypnum imponens facies	--	--	X	--	--
Hypnum curvifolium facies	--	--	X	--	--
Anomodon attenuatus	--	--	--	X	X
A. Rugelii facies	--	--	X	--	X
Tetraphis pellucida	--	--	X	--	--
Brachythecium oxycladon	--	--	--	X	--

2. HALESIO-SACCHARODENDRETUM (Peawood-Sugar Maple Association)

In the cove hardwoods forest type study this combination of dominants was met with occasionally. The sugar maple is found in various combinations with other dominant species and is even the sole dominant of certain stands. In so far as the Greenbrier and Mt. LeConte regions of the Great Smoky Mountains are concerned, sugar maple with beech codominant (a widespread climax type of many American ecologists) does not occur in so far as the authors know. When beech occurs as codominant it is usually with hemlock on the somewhat drier ridges of the broad valleys at elevations around 2,500-3,000 ft. The sugar maple-peawood combination is usually found on well-drained slopes just far enough from the valley floor to be above the hemlock and rhododendron dominance.

Our bryophytic studies of this forest type were made at 2,700 ft. elevation on the Woolly Tops Branch of the Little Pigeon River in Greenbrier. The composition of the tree layer at this station is given in Table 16.

a. *Terrestrial communities:*

The absence of terestrial bryophytic communities is explained in the same manner as that employed for the *Aesculo-Tilietum,* the very heavy coverage of the herbaceous layer.

b. *Epilithic communities: Thuidium delicatulum* union
: *Brachythecium oxycladon* union
: *Anomodon attenuatus* union
: *Hypnum curvifolium* facies
: *Grimmia pilifera* union

TABLE 16

The composition of the tree layer, Halesio-Saccharodendretum, 2,700 ft. elevation on Woolly Tops Branch, Greenbrier. Based on 4,200 sq. m.

Species	Basal area in sq. ft.	Per cent
Saccharodendron (Acer) barbatum	109.8	55.2
Halesia monticola	53.6	26.9
Tsuga canadensis	14.4	7.2
Tilia neglecta	7.3	3.7
Hicoria cordiformis	7.2	3.6
Aesculus octandra	3.5	1.7
Betula allegheniensis	1.8	.9
Cladrastis lutea	1.4	.7
Padus vriginiana	---	---
Cynoxylon (Cornus) floridum	---	---
	199.0	100.0

The bryophytic communities of 18 erratic boulders under this forest type were examined by means of 0.1 sq. m. quadrats. This investigation revealed 10 stands of the *Thuidium delicatulum* union and one to four stands of the four other unions, Table 17. The *Thuidium* union proper is composed of a very small number of species, however, island-like inclusions not yet overgrown by *Thuidium* bring the list up to 18 species. Four of these species could not be determined from the material available and so are cited only by their generic names. The *Brachythecium, Anomodon,* and *Hynum* communities are closely related sociologically but are distinct as to their dominance. The *Grimmia* union is a more open type of community characteristic of steep rock faces. At least 10 of the species in the table just cited may occur locally as dominants over small areas, constituting fragmentary communities. These apparently unstable relationships were ignored in our analyses.

c. *Epixylic communities: Thuidium delicatulum* union
: *Mnium affine* var. *ciliare* union
: *Hypnum* union
curvifolium facies
imponens facies
Heterophyllum nemorosum facies
: *Tetraphis pellucida* union

The bryophytic communities on 28 logs were examined by means of 0.1 sq. m. quadrats. The *Thuidium* union was the most frequent community dominated by one species. However, 16 communities dominated by species of *Hypnum* were encountered. They were classified under three divisions according to which species chanced to dominate, Table 18. The union with *Tetraphis pellucida* as the sole member is a widespread one found on the sides and lower parts of logs, characteristically occupying a zone below the large pleurocarpous mosses on the tops of the logs. It is found occasionally on wood of many species of trees under nearly all moist forest types.

TABLE 17

Thuidium delicatulum, Brachythecium oxycladon, Anomodon attenuatus, Hypnum curvifolium, and Grimmia pilifera communities on rocks under Halesio-Saccharodendretum, sampled by 0.1 sq. m. quadrats.

	Thuidium union										Hypnum facies
	3	4	5	6	11	12	13	14	17	18	8
Thuidium delicatulum	**5**	**5**	**5**	**5**	**3**	**5**	**5**	**5**	**5**	**5**	**2**
Hypnum curvifolium											**3**
Brachythecium oxycladon	x	x			**3**			x			
Hylocomium brevirostre					x					x	
Metzgeria sp?					x						
Fissidens cristatus					x						
Plagiochila sp?					x						
Anomodon attenuatus						x	1				
Amblystegium sp?						x					
Dicranum fulvum						x					
Leucolejeunea clypeata						x					x
Hedwigia ciliata						x					
Mnium affine var. *ciliare*							x	x			
Lophocolea heterophylla								x			
Hypnum molluscum									x		
Diphyscium sessile									x		
Fissidens minutulus									x		
Calypogeia fissa									x		
Jubula pennsylvanica									x		
Brachythesium plumosum											x
Total coverage per cent	95	95	100	100	95	95	100	95	100	100	100

	Brachythecium union				Anomodon union			Grimmia union			
	7	9	10	13	1	15	16	5	6	11	12
Brachythecium oxycladon	**5**	**5**	**5**	**5**	2	x					
Anomodon attenuatus	1		x		**3**	**5**	**5**			x	
Grimmia pilifera								**3**	**3**		**3**
Grimmia gracilis										**5**	
Thuidium delicatulum	1	x	x	1	1	x				x	
Mnium affine var. *ciliare*	x	1									
Bryhnia novae-angeliae	x										
Trichostomum cylindricum	x										
Cephaloziella spinicaulis	x										
Brachythecium plumosum			1								
Hedwigia ciliata				x				x	x		
Plagiothecium Muellerianum				x							
Metzgeria hamata				x		1		2			2
Raphidostegium carolinanum					x						
Ulota americana								2			
Leucolejeunea clypeata								2			1
Dicranum fulvum								x	1		x
Amblystegium sp?									2		
Radula sp?									x		x
Microlejeunea laete-virens											x
Number of species	7	3	4	5	4	4	1	6	5	3	5
Total coverage per cent	100	100	95	100	90	95	100	65	60	95	70

TABLE 18

Thuidium delicatulum, Mnium affine ciliare, Tetraphis pellucida, and Hypnum curvifolium, H. imponens, and Heterophyllum nemorosum communities on logs under Halesio-Saccharodendretum, sampled by 0.1 sq. m. quadrats.

	Thuidium union										Mnium union				Tetraphis union	
	4	6	7	8	15	16	22	26	27	28	1	5	11	19	14	17
Thuidium delicatulum	**5**	**4**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	2	1	2	x		
Mnium affine var. *ciliare*		**3**	x	x	x	x				1	**4**	**5**	**5**	**5**		
Tetraphis pellucida															**4**	**5**
Hypnum curvifolium	1		x	x	1	x	1	x	x	1	x		1	x		
Hylocomium brevirostre					x		x									
Heterophyllum nemorosum							x									
Hypnum imponens							x									
Brachythecium oxycladon										x	x	1				
Amblystegium varium										x						
Total coverage per cent	(100% unless otherwise indicated)										90	95			60	85

	Hypnum union															Heterophyllum nemorosum facies
	curvifolium facies										imponens facies					
	3	9	10	11	12	18	22	24	25	28	2	13	20	21	23	17
Hypnum curvifolium	**3**	**5**	**4**	**5**	**5**	**5**	**5**	**5**	**5**	**4**			x			x
Hypnum imponens	2										**5**	**5**	**5**	**5**	**5**	
Heterophyllum nemorosum	x					x					x		x			**5**
Thuidium delicatulum	x	1	**3**	2	1	x	2	x	x	2						x
Mnium affine var. *ciliare*		x	1	x	x				x							
Dicranum scoparium						x						x			x	
Brotherella recurvans						x										
Brachythecium oxycladon									x	x						
Leucobryum glaucum													1			
Total coverage per cent	(100% unless otherwise indicated)														95	

d. *Corticolous communities: Anomodon attenuatus* union
: *Neckera-Leptodon trichomitrion* facies

Five tree-butts of the sugar maple, *Saccharodendron barbatum,* were mapped to a height of 1 m. above the soil line. No tree-butts of the peawood, *Halesia monticola,* were mapped as in all cases the bryophytes on this tree were exceedingly scattered and only fragmentary communities could be recognized. This situation is due to the rapidity with which the bark of *Halesia* scales off. Only within three or four dm. of the soil is found a coverage approaching 50 per cent. Even on the sugar maple the dominant community of the lower part of the trunk, the *Anomodon* union, is not as extensive as that community usually is in the cove forest complex. This situation seems to be due to the slightly lower humidity of the forest type and to the harder, less absorbent, character of the bark.

The *Leptodon* facies, Table 19, is a community directly comparable with that dominated by *Neckera pennata,* both as to location and as to life-form.

TABLE 19

Anomodon attenuatus and Neckera-Leptodon trichomitrion communities on butts of Saccharodendron barbatum mapped to 1 m. above the soil.

	Anomodon union					Neckera-Leptodon facies	
	1	2	3	4	5	1	2
Anomodon attenuatus	**4**	**4**	**3**	**3**	**3**	x	x
Leptodon trichomitrion	x	x	x	x		**3**	**4**
Anomodon Rugelii	x	x	2	2	1	**3**	2
Anomodon rostratus	2	2	2	1	2	x	x
Brachythecium oxycladon	x	x	x	x	1		
Radula caloosiensis	x	x	x	x			x
Porotrichum allegheniense	x			x	x		
Thuidium delicatulum		x	x		x		
Amblystegium serpens			x	x	x	x	
Schwetschkeopsis denticulata		x		x			x
Rhodobryum roseum				x	x		
Anacamptodon splachnoides		x					
Plagiothecium sp?				x			
Cololejeunea Biddlecomiae				x			
Brachythecium sp?					x		
Anomodon tristis							x
Number of species	7	9	8	12	9	5	7
Total coverage per cent	80	75	75	75	80	65	70

Four fragmentary communities were found on *Halesia,* all of which are common on other species and on other substrata. They were dominated by *Anomodon attenuatus, A. rostratus, Thuidium delicatulum,* and *Brachythecium oxycladon.* Several additional species were observed on *Halesia,* occurring in small quantities: *Radula caloosiensis, Cololejeunea Biddlecomiae, Metzgeria furcata, Schwetschkeopsis denticulata, Anomodon tristis, Amblystegium serpens, Dicranum fulvum, Hypnum imponens,* and *Eurhynchium serrulatum.*

The top-limb flora, determined from recently fallen branches, consisted of the following: *Ulota crispa, Orthotrichum stellatum, Drummondia prorepens, Sematophyllum adnatum, Anomodon tristis, Porella platyphylloidea, Leucodon brachypus,* and *Leptodon trichomitrion.*

The communities of this forest type are summarized in Table 20.

3. LIRIODENDRO-TSUGETUM (Yellow Poplar-Hemlock Association)

One of the most interesting forest types of the Tsugion is that in which hemlock and yellow poplar codominate. This type presents one of the most magnificent forest scenes in Eastern America. In the primeval forest of the Great Smoky Mountains, virgin stands of this type are found in which numerous trees of *Liriodendron* reach a diameter breast high of six feet or more with an abundance of trees from 3-4 ft d.b.h. The hemlock usually

TABLE 20

Summary of the bryophytic communities of Halesio-Saccharodendretum.

Unions of	Substratum			
	Terrestrial	Epilithic	Epixylic	Corticolous
Thuidium delicatulum	--	X	X	--
Brachythecium oxycladon	--	X	--	--
Anomodon attenuatus	--	X	--	X
Grimmia pilifera	--	X	--	--
Hypnum				
curvifolium facies	--	X	X	--
imponens facies	--	--	X	--
Heterophyllum nemorosum facies	--	--	X	--
Mnium affine var. *ciliare*	--	--	X	--
Neckera-Leptodon trichomitrion facies	--	--	--	X

runs smaller but is frequently more than four feet in diameter. One tree was found on Chapman Fork near Lost Fork, in the Greenbrier region, which was nearly six feet through above the butt swell. Yellow poplar here frequently reaches a height of 140 ft. and sometimes 160 ft. or more with a columnar bole free of branches for 50-80 ft. Numerous species may be associated with these two dominants in this type but always in a subordinate role. Although the trees are widely spaced, this forest type attains the largest basal area of any in the Great Smoky Mountains, Table 21.

TABLE 21

Composition of the tree layer, Liriodendro-Tsugetum, 3,200 ft. elevation on Buck Fork, Greenbrier. Based on 5,400 sq. m.

Species	Basal area in sq. ft.	Per cent
Liriodendron tulipifera	151.9	41.5
Tsuga canadensis	99.8	27.2
Rufacer rubrum	31.8	8.6
Halesia monticola	28.0	7.6
Fagus grandifolia	23.3	6.3
Betula allegheniensis	16.7	4.5
Fraxinus americana	7.1	1.9
Tilia neglecta	6.9	1.8
Ilex monticola	.3	
Betula lenta	.2	
Magnolia Fraseri	.2	.6
Aesculus octandra	.1	
Svida alternifolia	--	
	366.3	100.0

The bryological studies in this forest type were made at 3,200 ft. elevation on Buck Fork in the Greenbrier region. Table gives the composition at this station. In making the forest type study, Cain (ms.) found several stands with hemlock and yellow poplar as codominants. In some the poplar predominated, in others the hemlock was more important. Hemlock as a

pure type occurs on ridges which are too well-drained for the poplar. Poplar as a pure stand seems to occur only in the form of second growth.

A very characteristic aspect of this forest is the almost complete lack of herbaceous growth. Only in openings produced by fallen trees is found an herbaceous layer. This is due to the heavy shade and root competition produced by the tree canopy and the frutescent layer of *Rhododendron* and *Kalmia* which usually has a coverage in class 4 or 5. Perhaps the most characteristic herbs found scattered over the soil are *Mitchella repens* and *Oxalis montana*. Occasionally one sees plants of *Monotropa uniflora, Trillium undulatum, Dryopteris intermedia,* etc. Other typical cove hardwoods species of herbs are found in the moss communities on the tree-butts.

a. *Terestrial communities:* As described above, the heavy shade and litter eliminates the bryophytic unions on the peaty soil, only fragmentary communities being found.

b. *Epilithic communities:* *Thuidium delicatulum* union
: *Hylocomium brevirostre* union
: *Mnium affine* var. *ciliare* union
: *Dicranum fulvum* union
: *Brotherella delicatula* facies
: *Radula Sullivantii* union

The bryophytic communities were examined on 23 erratic boulders by means of 0.1 sq. m. quadrats. Ten of the boulders showed top communities of the *Thuidium* union and 10 others of the *Hylocomium* union. Two other top communities were encountered and two side communities on the steep slopes. There are no especially distinctive features among the communities. It is worth calling attention to the fact that the *Brotherella* facies is dominated by *Brotherella delicatula,* a species not encountered elsewhere in the study. This is likewise true of *Radula Sullivantii* found on rock No. 19. The data obtained during this study are shown in Table 22.

TABLE 22

Thuidium delicatulum, Hylocomium brevirostre, Mnium affine ciliare, Brotherella delicatula, Dicranum fulva, and Radula Sullivantii communities on rocks under Liriodendro-Tsugetum, sampled by 0.1 sq. m. quadrats.

	Thuidium union									
	4	9	11	12	14	15	17	20	22	23
Thuidium delicatulum	**4**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**4**	**5**
Hylocomium brevirostre	**3**	1	1	1		2	2	1	2	1
Plagiothecium sp?		x								
Brotherella delicatula		x								
Heterophyllum nemorosum		x								
Mnium affine var. *ciliare*				x				1		
Hypnum molluscum									x	
Total coverage per cent	100	95	100	100	100	100	95	95	100	100

	Hylocomium union									
	1	2	3	5	6	7	8	13	18	21
Hylocomium brevirostre	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**
Thuidium delicatulum	1	1		1	x	x	x		x	x
Dicranum scoparium	x							x		
Scapania nemorosa	x									
Hypnum sp?	x									
Plagiothecium sp?			x					x		
Leucobryum glaucum								x		
Brotherella recurvans								x		
Total coverage per cent	100	95	85	100	95	100	100	100	80	100

	Dicranum union			Brotherella facies		Mnium union	Radula union
	1	9	13	9	16	10	19
Dicranum fulvum	**5**	**5**	**4**	x	x		x
Brotherella delicatula		x	2	**5**	**5**		
Mnium affine var. *ciliare*						**5**	
Radula Sullivantii							**5**
Thuidium delicatulum	x	x		x	x	x	x
Hylocomium brevirostre	x				x	x	
Metzgeria hamata	x						x
Jubula pennsylvanica	x						
Microlejeunea?	x						
Eurhynchium serrulatum	x						
Hypnum molluscum	x						x
Brachythecium plumosum	x						
Heterophyllum nemorosum				x			
Dicranum scoparium					x		
Leucobryum glaucum					x		
Total coverage per cent	95	95	80	95	95	95	90

c. *Epixylic communities: Thuidium delicatulum* union
: *Hypnum* union
Brotherella recurvans facies
Hypnum fertile facies
Heterophyllum nemorosum facies
: *Mnium affine* var. *ciliare* union
: *Dicranum fulvum* union
: *Tetraphis pellucida* union
: *Plagiothecium micans* union

The moss communities on ten logs were studied by means of 1 m. belts around the logs, as described in section III, on methods. The *Thuidium* union was found to be a characteristic log top community on nine of the logs, Table 23. The next most abundant type was that dominated by species of *Hypnum*, occurring on seven logs. Where *Thuidium* has developed a heavy mat on top of a log the species of *Hypnum* usually occur on the sides just below. The *Plagiothecium* union is a typical side community while *Tetraphis* occurs on the under slopes forming, however, in this group of samples, a heavy stand on only one log. There is nothing especially distinctive about these communities.

TABLE 23

Thuidium delicatulum, Brotherella recurvans, Hypnum fertile, Heterophyllum nemorosum, Mnium affine ciliare, Dicranum fulvum, Tetraphis pellucida, and Plagiothecium micans communities on logs under Liriodendro-Tsugetum.

	Thuidium union								
	2	3	4	5	6	7	8	9	10
Thuidium delicatulum	**5**	**4**	**5**	**5**	**4**	**4**	**4**	**4**	**5**
Hylocomium brevirostre	2	x		x	x	x	2		x
Mnium affine var. *ciliare*	1	1	x	x	x				1
Plagiothecium micans		x	x	x					
Dicranum scoparium		x				x			
Leucobryum glaucum		x			x				
Hypnum imponens		x							
Brotherella delicatula		x							
Brotherella recurvans			x		x		x	2	
Heterophyllum nemorosum			x			1	x	x	
Dicranum fulvum			x	x	1		x	x	
Brachythecium oxycladon				x					
Hypnum fertile					2	2	1		
Leucodon sp.?					x				
Dicranum montanum								x	
Frullania Asagrayana								x	
Rhodobryum roseum									x
Number of species	3	8	6	6	8	5	6	6	4
Total coverage per cent	100	80	95	100	95	95	95	90	100

	Hypnum facies							Tetraphis	Dicranum		Plagiothecium	Mnium
	1	2	3	6	7	8	9	1	5	9	5	10
Heterophyllum nemorosum	**5**			x		x	x	x		x		
Brotherella recurvans	x	**4**	**4**	**2**	x	**3**	**5**	x	2	x	x	
Hypnum fertile	x			**4**	**4**	**3**	x	2		x		
Tetraphis pellucida			1			1		**4**				
Dicranum fulvum						x	x		**4**	**3**		
Plagiothecium micans			x	x							**4**	x
Mnium affine var. *ciliare*					x				x		x	**5**
Hylocomium brevirostre	x			x	x	x						
Dicranum scoparium	x			x		x		x				
Thuidium delicatulum	x		x					x	x	x		x
Lophocolea heterophylla		x			x	x	x	x			x	
Leucodon sp?				x		x	x			x		
Dicranum montanum				x		x	x			**3**		x
Riccardia palmata					x	x	x					
**Cephalozia curvifolia*						2	x			x		
Jamesoniella autumnalis						x	x			x		
Rhodobryum roseum						x		x				x
Cephalozia media							x					
Leucobryum glaucum								x				
Plagiochila asplenioides								x				
Harpanthus scutatus								x				
Cephalozia bicuspidata								x				
Hypnum imponens										x		
Brachythecium oxycladon											1	x
Anomodon attenuatus											x	x

Radula sp?											x		
Metzgeria sp?											x		
Anomodon rostratus													x
Fissidens subbasilaris													x
Amblystegium varium													x
Porella platyphylloidea													x
Number of species	6	2	4	8	6	14	11	12	4	10	9	11	
Total coverage per cent	95	55	65	85	60	90	80	80	100	90	75	90	

d. *Corticolous communities: Brotherella recurvans* facies
: *Anomodon attenuatus* union
: *Anomodon rostratus* facies
: *Thuidium delicatulum* union
: *Brachythecium oxycladon* union
: *Mnium affine* var. *ciliare* union
: *Leucobryum glaucum* union

Five tree-butts of *Tsuga canadensis* and five of *Liriodendron tulipifera* were mapped to a height of 1 m. above the highest soil line. This made the area mapped 1.5-2.0 m. high on the low side, as these large trees stood on rather steep slopes. The yellow poplar trees which were mapped ranged from 13 ft. 3 in. to 16 ft. 6 in. in circumference at the top of the mapped area. The hemlock trees, although somewhat smaller, were nevertheless large trees, ranging from 10 ft. 6 in. to 12 ft. 6 in. in circumference.

TABLE 24

Brotherella recurvans, Anomodon attenuatus, A. rostratus, Thuidium delicatulum, Brachythecium oxycladon, Mnium affine ciliare, and Leucobryum glaucum communities on tree-butts of Liriodendron and Tsuga.

	Communities on Liriodendron												
	Anomodon union					Brachythecium union		Thuidium union					Mnium union
	1	2	3	4	5	2	3	1	2	3	4	5	1 5
Anomodon attenuatus	**3**	**4**	**4**	1	**3**	x	x					x	x
Anomodon rostratus	**3**	**3**	2	**4**	2	x	x			x	x	x	
Brachythecium oxycladon		x	x	x	x	**5**	2		x	x	x	x	x x
Bryhnia novae-angliae	x			x			**4**						
Thuidium delicatulum	1	x	x	x	x		x	**5**	**5**	**4**	**4**	**4**	2 x
Mnium affine var. *ciliare*	x				x		x		x		x	x	**4** **5**
Fissidens cristatus	x	x	x	x	x		1		x	x	x		
Campylium chrysophyllum	x	x	x		x					x		1	
Anomodon Rugelii	x		x		1								
Plagiothecium micans	x				2	x						x	
Neckera pennata		x	x	x									
Porotrichum allegheniense		x											
Zygodon sp?		x											
Hypnum molluscum			x	x									x
Brotherella recurvans				x					x	x		x	
Plagiothecium deplanatum						1							
Hylocomium brevirostre										x		2	
Rhodobryum roseum											x		
Total coverage per cent	75	90	90	75	90	90	95	90	95	70	90	75	100 85

	Communities on Tsuga													
	Brotherella facies					Leucobryum union				Thuidium union				
	1	2	3	4	5	1	2	3	4	1	2	3	4	
Brotherella recurvans	**3**	**5**	**3**	**4**	**5**			2	x		x			
Leucobryum glaucum	x	x	x	1	x	**4**	**5**	**4**	**3**		1	x		
Thuidium delicatulum	x	x	x	x	x					**5**	**4**	**5**	**5**	
Dicranum fulvum	2	1	x	x	x				2		x			
Bazzania trilobata	2	x	x	x	x						x			
Plagiothecium micans	x		x	x	x	x			x	x				
Hypnum reptile	1	x		x	x									
Dicranum montanum	x		1	x										
Hylocomium brevirostre										x				
Dicranum scoparium										x				
Total coverage per cent	80	80	50	60	85	65	95	60	60	90	70	90	90	

Two contrasts between *Tsuga* and *Liriodendron* are immediately apparent. The moss communities are more extensive on the softer more absorbent barked poplars than on the hemlock. The two species are dominated by different communities: *Anomodon* on *Liriodendron* and *Brotherella recurvans* on *Tsuga*, Table 24. The remaining communities listed occur either near the soil line on the trunks, in sinuses, or on the large roots where undoubtedly they are favored by a greater humidity and humus accumulation.

Several higher plants are associated with these bryophytic communities, sometimes with a coverage of class 2. The species observed were as follows: *Mitchella repens, Oxalis montana, Viola blanda, Tiarella cordifolia, Dentaria diphylla, Trillium erectum* var. *album, Alsine tennesseensis, Dryopteris intermedia,* and *Botrychium virginiana.*

Neckera pennata was observed to form a community on the trunks above

TABLE 25

Summary of the bryophytic communities of the Liriodendro-Tsugetem.

	Substratum				
Unions of	Terrestrial	Epilithic	Epixylic	*Corticolous* Hemlock	*Corticolous* Poplar
Thuidium delicatulum	--	X	X	X	X
Mnium affine ciliaris	--	X	X	--	X
Dicranum fulvum	--	X	X	--	--
Hylocomium brevirostre	--	X	--	--	--
Radula Sullivantii	--	X	--	--	--
Hypnum					
Brotherella delicatula facies	--	X	--	--	--
B. recurvans facies	--	--	X	X	--
Hypnum fertile facies	--	--	X	--	--
Heterophyllum nemorosum facies	--	--	X	--	--
Tetraphis pellucida	--	--	X	--	--
Plagiothecium micans	--	--	X	--	--
Leucobryum glaucum	--	--	--	X	--
Anomodon attenuatus	--	--	--	--	X
Anomodon rostratus facies	--	--	--	--	X
Brachythecium oxycladon	--	--	--	--	X

the level of the mapped area. The top-limb flora is made up of the following more common species: *Ulota crispa, Leucodon brachypus, L. julaceus, Anomodon attenuatus,* and *Frullania Asagrayana.* The following were less frequent, *Porella platyphylloidea, Dicranum* sp?, *Microlepeunea* sp?, *Frullania eboracensis, Anomodon tristis, Harpolejeunea ovata, Radula caloosiensis,* and *Metzgeria* sp?

The communities of this forest type are summarized in Table 25.

V. Discussion

A. Recognition and Delimitation of Communities

The general procedure in this work was to make quantitative analyses of the bryophytic unions for each substratum of each forest type. A tentative name was assigned to each community. On the basis of the statistical results regarding dominance (coverage classes) and homogeneity (constance or presence). Thus 34 communities, all of equal rank, were recognized at first. A comparative study of the floristic content and distribution of these community-entities, however, led to a revision. Many were relegated to the rank of subcommunity or facies of a union while some were later eliminated from consideration on the basis of their being a more or less isolated chance combination of species or dominants. In this manner the taxonomy of the communities was simplified and their relationships could be more clearly indicated. After the communities and sub-communities were ascertained the next effort was to group them into alliances. In this a combination of characteristics was used: the taxonomic and growth-form similiarity of the dominants; the similarity of their floristic assemblages and their characteristic substrata.

1. *Upper corticolous communities*

No quantitative study was made of the top-limb flora, that is, of the species characteristic of the canopy, in many cases over 100 ft. above the ground. Lists were prepared from recently blown down branches. The assembly of these lists in Table 26 reveals that *Ulota crispa (U. ulophylla)* is common to all six forest types studied, with a range in elevation from 2,700 to 6,500 ft. *Frullania Asagrayana* also is found to be widespread on the top-limbs of both the spruce-fir and the cove hardwoods. *Leucodon brachypus* is found on all deciduous types. A glance at the preceding tables shows that 17 of the 26 species of the top-limb flora are also members of the corticolous communities of the tree-butts. Also, five of these species are found as dominants of certain communities of the tree-butts. There are, however, certain distinctive species which have led to the decision that the top-limb flora constitutes a distinct union which should be named after its most widespread species, *Ulota crispa.*

Certain species form obvious communitites on the tree trunks above the mapped zone of the tree-butt and below the top-limb flora. It was impractical to reach this zone for careful analysis, but this much is sure: *Neckera pennata,* found on the tree-butt zone in the Fagetum grandifoliae subalpinum, is a common community forming species of the middle trunk heights in the cove

hardwood forest complex, occurring on *Aesculus, Tilia, Saccharodendron, Liriodendron,* etc. *Leptodon trichomitrion* is a frequent associate of *Neckera pennata* and sometimes dominates alone, especially at lower elevations and on the lower parts of tree trunks. In this region of the tree one also finds several of the plants of the top-limb flora: *Leucodon, Zygodon, Ulota, Frullania, Porella,* etc., in lesser abundance, together with certain of the tree-butt species which, under favorable conditions, extend upward into the middle trunk region: *Anomodon, Radula, Hypnum,* etc. As a consequence of the above considerations we have established a community classification which is found at the end of this section.

TABLE 26

The top-limb flora of Ulota crispa union.

	Subalpine			Cove hardwoods		
Elevation—	Abietum 6500	Piceetum 5000	Fagetum 4700	Aesculo-Tiliet. 3800	Halesio-Sacch. 2700	Lirio-Tsug. 3200
Ulota crispa	x	x	X	x	x	x
Frullania Asagrayana	XX	XX	–	X	–	x
Hypnum reptile	X	X	–	–	–	(–)
Paraleucobryum longifolium	X	x	–	–	–	–
Leptodontium excelsum	X	x	–	–	–	–
Zygodon viridissimus	X	x	–	–	–	–
Leucodon brachypus	–	–	XX	x	x	x
Ulota americana	–	–	–	x	–	–
Ulota americana var. *rufescens*	–	–	X–X	–	–	–
Porella platyphylloidea	–	–	X	–	x	x
Orthotrichum pumilum	–	–	X	–	–	–
Anacamptodon splachnoides	–	–	x	–	(–)	–
Platygyrium repens	–	–	x	–	–	–
Drummondia prorepens	–	–	x	–	x	–
Anomodon tristis	–	–	(–)	(–)	X	x
Radula caloosiensis	–	–	(–)	(–)	(–)	x
Frullania eboracensis	–	–	(–)	–	–	x
Anomodon attenuatus	–	–	–	X–X	X–X	XX
Leptodon trichomitrion	–	–	–	(–)	XX	–
Leucodon sciuroides	–	–	–	X	–	–
Orthotrichum stellatum	–	–	–	–	x	–
Sematophyllum adnatum	–	–	–	–	x	–
Leucodon julaceus	–	–	–	–	–	x
Harpolejeunea ovata	–	–	–	–	–	x
Dicranum sp?	–	–	–	–	–	x
Microlejeunea sp?	–	–	–	–	–	x
Metzgeria sp?	–	–	–	–	–	x
Number of species in top-limb flora:	6	6	7	5	8	13
Number of top-limb species found also on the tree-butts:	5	2	8	6	5	2

x Found only on the top-limbs in the particular forest type.
X Found in the top-limb flora and also on the tree-butts.
XX Found in the top-limb flora and as a dominant on tree-butts.
(–) A member of the top-limb flora elsewhere, but only on tree-butts in the particular forest type.
X–X A member of the top-limb flora elsewhere, but only on tree-butts in the particular forest type, where it is a dominant.

2. *Communities of large pleurocarpous mosses*

Several of the corticolous species of the tree-butts are found also on logs, rocks, or soil. With respect to the associated species, as opposed to the dominants, this is true even to a greater extent. This arises from the fact that obligate epiphloeodal (corticolous) species in this flora are quite rare, although many species find conditions for growth better and competition reduced on bark. Any taxonomic treatment of the remaining corticolous communities must then consider also those on other substrata. In attempting to sort these communities into a true classification it appears logical to attempt a grouping of those communities which are dominated by different species of the same genus. A consideration of *Hypnum* from this point of view leads to the treatment found on the next page. See also, Table 27.

TABLE 27

The comparative distribution of species of Hypnum.

Hypnum union, represented by 7 facies	A TLXC	P TLXC	F TLXC	AT TLXC	HS TLXC	LT TLXC
Brotherella recurvans	x.xx	..XX	....	....	..x.	.xXX
Heterophyllum nemorosum	....	..x.	....	..X.	..X.	.xX.
Hypnum imponens	....	..x.	..x.	..X.	..Xx	..x.
Hypnum fertile	....	..xx	..x.	..x.	....	..X.
Hypnum curvifolium	....	....	....	..X.	.XX.	....
Brotherella delicatula	....	....	....	....	....	.Xx.
Hypnum-Bazzania trilobata	.xx.	x.xX	....	....	....	...x
Additional species, not dominant:						
Hypnum molluscum	....	....	....	....	.x..	.x.x
Hypnum reptile	...x	..xx	....	....	....	...x
Hypnum sp?	....	....	....	....	....	.x..
Hypnum Crista-castrensis	x.xx	..xx	....	....	....	....
Calliergonella Schreberi	....	..x.	....	....	....	....

. Species absent.
x Species occurs as an associate.
X Species occurs as a community dominant.
Top line initials: A, Abietum; P, Piceetum; F, Fagetum; AT, Aesculo-Tilietum; HS, Halesio-Saccharodendretum; LT, Liriodendro-Tsugetum.
Second line initials: T, terrestrial; L, epilithic; X, epixylic; C, corticolous.

Altogether, there are 11 species of *Hypnum* (taken in the broad sense to include Brotherella, Heterophyllum, etc.) six of which are community dominants. No dominant species of *Hypnum* was found restricted to a single forest type and to a single substratum, although certain ones were predominantly of one situation. All in all, it seems best to refer to the various stands collectively as a single union in which the local dominance of one species may be recognized as a sub-community or facies at the discretion of the individual. One general impression is that wider observations in the Smoky Mountains will tend to confirm the essential ecological equivalence of these species, with the exception, perhaps, of *Hypnum Crista-castrensis*, which is obviously confined to the spruce-fir forest formation.

TABLE 28

The comparative distribution of species of the alliance Thuidiion, exclusive of Hypnum. Symbols as in the preceding table.

Alliance, Thuidiion delicatulae	A TLXC	P TLXC	F TLXC	AT TLXC	HS TLXC	LT TLXC
Thuidium delicatulum union	x.xx	..xx	.xx.	.XXX	.XXx	.XXX
Hylocomium splendens union	XxXX	X.xx	....	....	....	....
Hylocomium umbratum union	xxxx	....	....	....	....	....
Hylocomium brevirostre union	x...	....	.x..	.XXx	.xx.	.Xxx
Bazzania denudata facies	...X	...x	....	....	....	....
Anomodon attenuatus union	....	....	....	.xxX	.X.X	..xX
Anomodon Rugelii facies	....	....	...X	..xX	...x	...x
Anomodon rostratus facies	....	....	....	...x	...x	..xX
Anomodon tristis	....	....	...x	...x	...x	....
Mnium affine var. *ciliare* union	....	....	..x.	.XX.	.xX.	.XXX
Brachythecium oxycladon union	....	....	...x	.xxX	.Xxx	..xX

If we now consider several other species which have a similar life-form and distribution (Table 28), we again find that, in the main, they range over several forest types and substrata. *Hylocomium splendens,* both as a species and as a community dominant, is restricted essentially to the spruce-fir forest. This is likewise true of the less important species, *H. umbratum* and *Bazzania denudata. Hylocomium brevirostre,* in the cove hardwoods, plays a role comparable to *H. splendens* in the spruce-fir. The Anomodons are restricted to the broad-leaf forests. Since two or more of the species of *Anomodon* may frequently occur together, and since *A. attenuatus* is both more widespread and more frequently a dominant, it seems wise to name the community after it, allowing the other species to designate sub-communities when they occur locally as dominants. *Thuidium delicatulum* is the most widespread member of the group, attaining community dominance, however, only in the cove hardwoods. Because of its ecological amplitude it seems wise to name the alliance after it. Because of their floristic affinities, the Mnium and the Brachythecium unions are also placed in this alliance.

The organization of the two alliances just described, as now recognized by us, is as follows:

A. NECKERO-ULOTION ALLIANCE OF UNIONS
(Top-limb communities)
1. Ulota crispa union
   a. *Leucodon brachypus* facies
   b. *Frullania Asagrayana* facies
   c. *U. americana* facies
(Middle trunk communities)
2. Frullania Asagrayana union
3. Neckera pennata union
   a. *Leptodon trichomitrion* facies

B. THUIDIION DELICATULAE ALLIANCE OF UNIONS
1. Hypnum union
   a. *Brotherella recurvans* facies
   b. *Heterophyllum nemorosum* facies
   c. *Hypnum imponens* facies
   d. *H. fertile* facies
   e. *H. curvifolium* facies

f. *Brotherella delicatula* facies
g. *Bazzania trilobata* facies
2. Hylocomium splendens union
a. H. *Bazzania denudata* facies
3. Hyloclomium brevirostre union
4. Anomodon attenuatus union
a. *A. Rugelii* facies
b. *A. rostratus* facies
5. Thuidium delicatulum union
6. Brachythecium oxycladon union
7. Mnium affine var. ciliare union

In this manner 23 of the 34 communities are classified under two alliances, 10 unions and 14 facies. The remaining communities are less frequent and less well-known. Some are unions of early stages of succession, as **Cephalozia* and **Sphenolobus*, and some are characteristic of steep rock faces, as *Grimmia* and *Hedwigia*. These unions are, in the main, dominated by small liverworts or by acrocarpous mosses. Their taxonomic disposition will have to await further bryocoenological studies.

REFERENCES

AMANN, J. 1896—Étude de la Flore Bryologique du Haut—Jura Moyen. Bull. Soc. Botan. Suisse **6**.

———1928—Brygéographie de la Suisse. Beiträge zur Kryptogamenflora der Schweiz. Bd. **6**:1-453.

APINIS, A. AND A. M. DIOGUCS. 1933-5—Data on the ecology of bryophytes. I. Acidity of the substrata of Hepaticae. II. Acidity of the substrata of Musci. Acta Horti Botan. Univ. Latviensis **8-10**.

BIZOT, M. 1937—Bryogéographie de la Côte-D'Or. Dijon.

BRAUN-BLANQUET, J. 1932—Plant Sociology (Trans. by G. D. Fuller and H. S. Conard). McGraw-Hill, New York.

BRAUN-BLANQUET, J. AND J. PAVILLARD. 1925—Vocabulaire de sociologie végétale, 3rd. ed. Montpelier.

BUCH, H., A. W. EVANS, AND FR. VERDOORN. 1937 (1938)—A preliminary check list of the Hepaticae of Europe and America (North of Mexico). Ann. Bryol. **10**:3-8.

CAIN, STANLEY A. 1932—Concerning certain phytosociological concepts. Ecol. Monogr. **2**:475-508.

———1936—Synusiae as a basis in plant sociological field work. Amer. Midl. Nat. **17**(3):665-672.

CAIN, STANLEY A. AND WM. T. PENFOUND. 1938—Aceretum rubri: the red maple swamp forest of Central Long Island. Amer. Midl. Nat. **19**(2):390-416.

CAJANDER, A. K. 1909—Über Waldtypen. Acta forestalia Fennica **1**. (Also in Fennia **28**.)

———1926—The theory of forest types. Acta forestalia Fennica **31**.

COCKAYNE, L. 1926—Ecological-economic investigation of the New Zealand Nothofagus forests. In "Aims & Methods in the Study of Vegetation," pp. 330-340. London.

CONARD, H. S. 1932—A boreal moss community. Iowa Acad. Sci. **39**:57-61.

COOPER, W. S. 1912—The ecological succession of mosses as illustrated upon Isle Royale, Lake Superior. Plant World **15**:197-213.

———1928—Seventeen years of successional change upon Isle Royale, Lake Superior. Ecology **9**:1-5.

DAVY DE VIRVILLE, A. 1927-28—L'action du milieu sur les Mousses. Rev. gén. d. Bot. **39**:364 ff., **40**:30 ff.

DUDGEON, W. 1923—Succession of epiphytes in the Quercus incana forest at Landour, Western Himalayas. Jour. Indian Bot. Soc. **3**:270-272.

DU RIETZ, G. E. 1930—Vegetationsforschung auf soziations-analytischer Grundlage. Abderhaldens Handb. Biol. Arbeitsmeth. **11**, **5**:293-480.

EMIG, W. H. 1930—A society of bryophytes. Bryol. **33**:11.

GAMS, H. 1934—Beiträge zur Kenntnis der Steppenmoose. Ann. Bryol. **7**:37-56.

GLEASON, H. A. 1936—Is the synusia an association? Ecology **17**(3):444-451.

GLENN, G. G. AND W. H. WELCH. 1931—Ecological relationships of the most common mosses in a certain vicinity near Bloomington, Indiana. Proc. Ind. Acad. Sci. **40**:87-101.

GROUT, A. J. 1903—Mosses with Hand-lens and Microscope. Newfane, Vermont.

———1928-1937—Moss Flora of North America North of Mexico. **1-3**. Newfane, Vermont.

HEIMBERGER, C. C. 1934—Forest-type studies in the Adirondack region. Cornell Univ. Agric. Exp. Sta. Mem. **165**:1-122.

HERZOG, T. 1926—Geogrgaphie der Moose. Fischer, Jena.

IKENBERRY, G. J. 1936—The relation of hydrogen-ion concentration to the growth and distribution of mosses. Amer. Jour. Bot. **23**:271-279.

KLEIST, C. 1929—Recherches phytosociologiques sur les toubières de la région des dunes de la rise droite de la Vistule au environs de Varsovie. Bull. Internat. Acad. Polon. Sci. de Cracovie, Sér. **B**, **1929**:41-104.

KOPPE, FRITZ. 1929—Das Montane Element in der Mossflora von Schleswig-Holstein. Annales Bryol. **2**:35-66.

———1932—Eine Mossgesellschaft des feuchten Sandes. Ber. Deutsch. Bot. Ges. **50**:502-516.

LIPPMAA, T. 1933—Grundzüge der pflanzensoziologischen Methodik nebst einer Klassifikation der Pflanzen-Assoziationen Estlands. Esthonian, with German summary. Acta Inst. et Horti Botan. Univ. Tartuensis **3**(4):1-169.

———1934—Sur la genèse de la flore nouvelle des îlots se formant par suite d'elevation séculaire sur la côte Nord-Ouest de Saaremaa (Estonie) In the Esthonian with French summary. Acta Inst. et Horti Botan. Univ. Tartuensis **4**(1-2):1-38.

———1934—La méthode des associations unistrates et la systèm écologique des associations. Acta Inst. et Horti Botan. Univ. Tartuensis **4**(1-2):1-6.

———1935—Une analyse des forêts de l'île estonienne d'Abruka (Abro) sur la base des associations unistrates. Acta Inst. et Horti Botan. Univ. Tartuensis **4**(1-2):1-97.

MARKGRAF, F. 1928—Kleines Praktikum der Vegetationskunde. Biol. Studienbücher **4**:1-64. Berlin.

MEUSEL, HERMANN. 1938—Neuere Arbeiten über die Verbreitung und Vergesellschaftung Niederer Pflanzen, insbesondere von Moosen und Flechten. Hercynia, Abh. Bot. Ver. Mitteldeutschlands, **1**(2):327-332.

MONTGOMERY, C. E. 1931—Ecology of the mosses of Grand de Tour region of Illinois, with special reference to pH relations. Bot. Gaz. **91**:225-251.

NICHOLS, G. E. 1913—The vegetation of Connecticut. II. Virgin forests. Torreya **13**:199-215.

———1915—The vegetation of Connecticut. IV. Plant Societies in lowlands. Bull. Torrey Bot. Club **42**:169-217.

———1916—The vegetation of Connecticut. V. Plant societies along rivers and streams. Bull. Torrey Bot. Club **43**:235-264.

OCHSNER, F. 1927—Studien über die Epiphytenvegetation der Schweiz. Jahrb. St. Gallisch. Naturw. Gesellsch. **63**(2):1-108.

OLSEN, C. 1917—Studies on the succession and ecology of epiphytic bryophytes on the bark of common trees in Denmark. (English summary). Botan. Tidsskrift **34**:313-342.

PESSIN, L. J. 1925—An ecological study of the polypody fern, Polypodium polypodioides, as an epiphyte in Mississippi. Ecology **6**:12-38.

PLITT, C. C. AND L. J. PESSIN. 1924—A study of the effect of evaporation and light on the distribution of lichens. Bull. Torrey Bot. Club **51**:203-210.

ROBINOVE, J. J. AND C. D. LARUE. 1928—The hydrogen-ion concentration of habitat of the bryophytes and pteridophytes of Douglas Lake region. Proc. Mich. Acad. Sci. Arts Letters **9**:273-287.

RÜBEL, E. 1930—Pflanzengesellschaften der Erde. Huber, Bern.

SHREVE, F. 1911—Studies on Jamaican Hymenophyllaceae. Bot. Gaz. **51**:184-209.

———1914—A montane rain-forest. Carnegie Inst. Wash. Publ. **199**.

SIRGO, V. 1935—Plant unions of the swamps at the mouth of the river Emajogi. Esthonian, with English summary. Acta Inst. et Horti Botan. Univ. Tartuensis **4**(3-4):1-63.

TAYLOR, A. M. 1920—Ecological succession of mosses. Bot. Gaz. **69**:449-491.

VAN OYE, P. 1921—Influence des facteurs climatique sur la répartition des épiphytes a la surface des troncs d'arbres a Java. Rev. Gén. Bot. **33**:161-176.

VERDOORN, FR. 1932—Manual of Bryology. Nijhoff. The Hague.

WATSON, W. 1932—The bryophytes and lichens of moorland. Jour. Ecol. **20**:284-313.

———1936—The bryophytes and lichens of British woods. I. Beechwoods. II. Other woodland types. Jour. Ecol. **24**:139-161; 446-478.

WILSON, B. L. 1936—A bryocoenological study of some epiphytic mosses of a Central Indiana woods. Butler Univ. Bot. Studies **3**(10):149-171.

WISNIEWSKI, T. 1929—Les associations des Muscinées épiphytes de la Pologne, en particulier celles de la foret vierge de Biatowieza. Bull. Internat. Acad. Polon. Sci. de Cracovie, Sér. **B**, **1929**:293-342.

Bark Factors Affecting the Distribution of Corticolous Bryophytic Communities[1]

W. D. Billings and W. B. Drew

Introduction

The intensive study of the composition and ecology of bryophytic communities has been markedly lacking in America compared to the great amount of bryocoenological research which has been carried on by Europeans. This lack, perhaps, may be explained by the fact that we do not yet know much about the structure and environment of the larger forest communities which, as a result, occupy the greater part of the American ecologist's time and interest. However, the forest community is found almost always to be a phytocoenosis composed of two or more synusiae. It is not possible to understand truly the phytocoenosis as a whole unless each synusia has been thoroughly studied. It is impossible to isolate any synusia from its phytocoenosis and to treat it as a separate *association* (Gleason, 1936). On the other hand, each synusia, no matter how small or obscure, has some effect on the development and structure of the whole phytocoenosis and, therefore, intensive studies of the several synusiae are the foundation-stones in any research which would truly portray the life and composition of a complex forest community.

In the virgin hardwood forests of the Great Smoky Mountains of eastern Tennessee, the bryophytic synusia not only occurs on rocks, rotting logs, and occasionally soil, but also extends some distance up the trunks of the large trees. The bryophyte layer in all of these types of habitats is made up of readily discernable communities or "unions" (Sirgo, 1935) dominated by one or two species. The present paper is confined to a study of only those bryophytic unions on the trunks of living trees. It is an attempt to learn the effect of various bark factors on the distribution of these unions on the trunks of several species of trees of the dominant synusia. Definite knowledge of the ecology of these bryophytic micro-communities should lead to a better understanding of this synusia and its place in the virgin forest phytocoenosis.

Plan of Study and Methods

The present investigation was carried out on corticolous bryophyte communities in the Greenbrier Region of the Great Smoky Mountains in eastern Tennessee. This region lies on the western slope of the main ridge of the Smoky range which rises to a height of over 6,000 feet all along the eastern

---

1 Contributions from the Botanical Laboratory, The University of Tennessee, n. ser. 25.

The research upon which this paper is based was carried on in the school year 1936-37 while the authors held temporary teaching positions in the University of Tennessee.

edge of the Greenbrier area. Mt. Guyot, with an elevation of 6,621 feet, stands at the northeastern corner of this large expanse of wilderness. The mountain coves or valleys, between 2,000 and 4,500 feet elevation, in this area are occupied by a mixed hardwood forest. This virgin cove hardwood forest has been divided into two alliances and several associations by Cain (1938). Among the associations are the Aesculo-Tilietum or Buckeye-Basswood association, the Halesio-Saccharodendretum or Peawood-Sugar Maple association, and the Liriodendro-Tsugetum or Yellow Poplar-Hemlock association from their respective dominants.

Many of the trees in these hardwood associations are abundantly covered with epiphytic bryophytes, especially around the base of the trunk. Some of these epiphytic communities have been studied by Cain and Sharp (1938). They have noticed striking differences between the types of these communities on Liriodendron and those occurring on Tsuga. The present study is an outgrowth of an attempt to discover the reason or reasons for the occurrence of different types of bryophytic communities on several species of trees in the Liriodendro-Tsugetum.

The exact location chosen for study is at an altitude of about 3,200 feet on Ramsey Fork, a tributary of Little Pigeon River. The forest at this point is strictly virgin and very luxuriant. The trees are very large, some of the trees of Liriodendron being as much as six feet in diameter breast high and tall in proportion. The principal overstory trees, in addition to *Liriodendron tulipifera,* are *Tsuga canadensis, Aesculus octandra, Fraxinus americana, Tilia neglecta, Betula lutea, Fagus grandifolia,* and an occasional *Castanea dentata.* The stream at this point falls precipitously between steep, rocky, vegetation-covered banks about 40 feet high. Back of these banks are sloping terraces from 100 to 400 feet wide, which rise gradually upward away from the stream to the steep ridges forming the boundaries of the Ramsey watershed. The valley here runs in an approximately northeast-southwest direction with the flow of water being in the latter direction.

Ten trees were selected for intensive study. These included four trees of Liriodendron, two of Tsuga, one *Fraxinus americana,* one *Aesculus octandra,* one *Fagus grandifolia,* and one *Castanea dentata.* All but the last were on the south side of the stream, either on the terrace or on the steep stream bank. The Castanea was located on the north terrace.

On each tree, six feet above the highest soil line, a string was drawn tightly about the trunk. Thumbtacks were placed on this string to denote the north, east, south, and west sides. The moss cover of the tree butt was then mapped to scale on cross-section paper.

Heretofore, the classification and terminology of bryophytic synusial communities followed by American students (i.e. Wilson, 1936) has largely been based on the system proposed by Gams (1932). In this mapping, however, the bryophyte cover was subdivided into synusial communities or "unions" as designated by Sirgo (1935) and Cain and Penfound (1938). These unions are usually dominated by one or two species and are very homogeneous within themselves. Coverage estimates for individual species in each union on each

tree-species were made at the time of mapping. Collections were taken from each union on every tree to check all identifications.

The bark samples were taken with a canvas-punch. This sampler was driven into the bark to the depth of about 7 or 8 millimeters and brought out with a circular bark sample of that thickness and about 2 centimeters in diameter. Samples were taken usually in six places on the tree; three on the south face of the trunk and three on the north face. The three locations on each face were at the following heights: 3 feet, between 4 and 5 feet, and 6 feet. The 3-foot-height, in every case but one or two, was moss-covered and the moss was carefully removed to obtain the samples. The 4 to 5-foot-height was usually on the margin between the moss cover and bare bark. The 6-foot-height samples, in all cases, were taken from bare bark. Nine samples were taken from each of the six locations on any one tree. These nine samples were placed immediately in three air-tight, metal weighing-cans and taken into the laboratory. There they were weighed, dried at 110° C. for 48 hours, re-weighed, and the average field moisture content calculated for the bark at that position on the trunk. Such field moisture samples were collected from trees No. 1 (Liriodendron), No. 2 (Aesculus), and No. 3 (Tsuga) on October 25, 1936. Samples were taken from trees No. 4 (Liriodendron), No. 5 (Tsuga), and No. 6 (Liriodendron) on November 1, 1936. Those from trees No. 7 (Liriodendron), No. 8 (Fraxinus), and No. 9 (Fagus) were obtained on November 8, 1936. As may be noticed, on each of these collection days samples were taken from a Liriodendron for purposes of comparison. The samples from the Castanea were not obtained until April 4, 1937 and so cannot be compared with those from other tree species as far as field moisture is concerned.

Two series of field moisture collections were taken from Tree No. 6, a Liriodendron, on March 21, 1937. The first of these was a vertical series taken on the southeast face at 6-inch intervals from ground-level to a height of 6 feet. The moss union covering each point of collection was recorded. The second series was horizontal at a height of 3 feet and extended all the way around the trunk at intervals of one foot. Records were also made in this series as to the moss union covering each collection.

Experiments were also carried out on the various kinds of bark to discover the water-holding capacity, rate of drying-out, and rate of absorption from a saturated atmosphere. In investigating the water-holding capacity, two series of samples were run. In each series, samples from a Liriodendron were used for comparative purposes. Three unbroken bark cores from each trunk location were soaked for 48 hours in water. At the end of this time, they were allowed to drain for 15 minutes and then all three were placed in a closed metal can and weighed. The water-holding capacity of the bark was determined from this net weight, after the oven-dry weight of these three cores had been determined at the end of the experiment. After the wet cores had been weighed, the lid was removed from the can and the bark exposed to quiet air in the laboratory. Weighings were made at various intervals until the samples were thoroughly air-dry. The cans were placed in an oven at 110° C.

for 48 hours and then re-weighed to determine the oven-dry weight of the samples used.

After being oven-dried, the same sets of samples were used to determine the rate of water-absorption from a saturated atmosphere. The open cans were placed in an apparatus consisting of a wire tray over a dish of warm water, all contained in a covered, glass moist-chamber which had its ceiling covered with cotton-packed gauze to prevent drops of water from condensing and falling into the cans. The whole apparatus was quickly put into an electric refrigerator with a fairly constant temperature of about 6° C. The air was immediately saturated and remained so throughout the experiment. The cans were removed for weighings at various intervals until the curve of absorption began to level off.

The pH of the bark was determined by the quinhydrone electrometric method. Determinations were made on pulverized bark from each location on every tree.

Results

A. Bryophytic Communities

In the following descriptions of bryophytic unions, it will be noted that certain ones occur infrequently on the species of trees studied. As a result of the infrequency of several of these unions, it has not seemed necessary to present data for presence classes of the component species. Other phytosociological concepts such as "frequency," "constance," etc. cannot be applied in the present analysis since the communities were not studied on a unit area basis. "Sociability" classes were not assigned for the various species of bryophytes because of the obvious difficulty of delimiting the extent of an individual plant, especially of the hypnoid type.

I. BRYOPHYTIC UNIONS ON DECIDUOUS TREES

1. *Neckera pennata* Union. This union occurs commonly on the bare bark of the deciduous trees investigated. It may grow on the trunk at considerable heights from the ground, but no effort was made in this study to include upper trunk and crown communities. The lower limits of this union are usually those of the bare bark itself, though on only one face of the trunk. On most of the deciduous trees where Neckera grew below the six-foot-level, it occurred on the bare bark on the northwest face of the trunk. Table 1 records the occurrence of the *Neckera pennata* union on the various deciduous trees studied, the species of which the community is composed and their presence classes.

From the table, it will be noted that except on Fagus and Castanea, the *Neckera pennata* union consists mostly of Neckera itself. On Castanea, no Neckera was observed but on that tree there was developed a community very similar to it. The most important components of this community (marked "mixed" on the map, Fig. 1) are included in the table, but there were a few other bryophytes of minor significance in the union as well as some lichens,

TABLE 1

Occurrence of the *Neckera pennata* union.

Species list	Lir. 1	Lir. 4	Lir. 6	Lir. 7	Aes.	Fra.	Fag.	Cas.	Pr.
1. *Neckera pennata*	x	x	x	–	x	x	x	–	4
2. *Campylium chrysophyllum*	–	x	x	–	–	–	x	x	3
3. *Radula complanata*	–	–	–	x	–	–	–	x	2
4. *Anomodon attenuatus*	–	–	x	–	–	–	x	x	2
5. *Anomodon rostratus*	–	–	–	–	–	–	x	x	2
6. *Brachythecium oxycladon*	–	–	–	–	–	–	x	x	2
7. *Forsstroemia trichomitria*	t*	–	–	–	t	t	–	x	1

* The letter "t" indicates that the moss so designated grew just above the six-foot-mark.

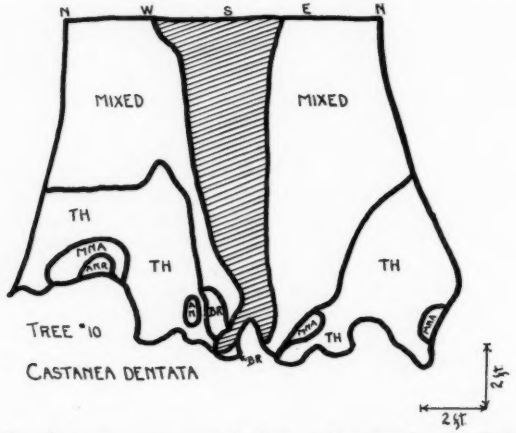

Fig. 1. Bryophytic communities on the butt of *Castanea dentata*. TH=*Thuidium delicatulum*, MNA=*Mnium affine* var. *ciliare*, AN=*Anomodon attenuatus*, ANR=*Anomodon rostratus*, BR=*Brachythecium oxycladon*. "Mixed" refers to a community similar in structure to the *Neckera pennata* union of other trees, but lacking the presence of Neckera. Cross-hatched areas= bare bark.

the identity of the latter not being determined. Finally, on Liriodendron No. 7 there was represented only a *Radula complanata* facies of the Neckera union.

2. *Campylium chrysophyllum* Union. This bryophyte community, when developed on the butt of a deciduous tree, usually grows from three to six feet from the ground. Of the different species of deciduous trees studied, only two Liriodendrons and a Fraxinus supported a distinct Campylium union. Nevertheless, Campylium itself was a very common component in many other communities, being represented to some extent in nearly every union studied on the deciduous species of trees and, more rarely, on Tsuga. On Liriodendron, an interesting relationship between the development of Campylium and *Anomodon attenuatus* unions was observed. Thus, on Liriodendron No. 4 as may be noted from the map (Fig. 2), Campylium is limited in its develop-

ment to a small area of bark adjacent to the Neckera and *Anomodon attenuatus* unions. On this same tree, the latter community is extremely well-developed and is of high coverage on the butt. Then, comparing the preceding situation with that on Liriodendron No. 6 (map, Fig. 3), it may be noted that the relations of the two communities are reversed with Campylium of the greatest coverage and *Anomodon attenuatus* of a limited distribution on the butt. Very nearly the same situation may be observed on Fraxinus (map, Fig. 4). Apparently, Campylium may only form an extensive community on the butt of a deciduous tree when the Anomodon union is limited in its extent.

The species of bryophytes which were found in the Campylium union are noted in the following list where they are arranged in order of their relative importance in the community: *Campylium chrysophyllum, Anomodon attenuatus, A. rostratus, A. Rugelii, Brachythecium oxycladon, Fissidens cristatus, Forsstroemia trichomitria, Thuidium delicatulum, Homalotheciella subcappillata, Radula complanata,* and *Metzgeria conjugata.*

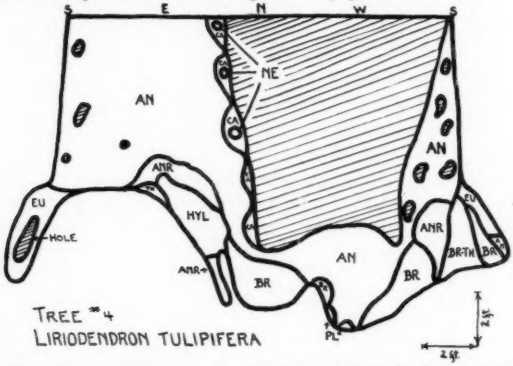

Fig. 2. Bryophytic communities on the butt of *Liriodendron tulipifera* No. 4. AN=*Anomodon attenuatus*, ANR=*Anomodon rostratus*, CA=*Campylium chrysophyllum*, NE=*Neckera pennata*, TH=*Thuidium delicatulum*, HYL=*Hylcomium brevirostre*, EU=*Eurhynchium strigosum*, BR=*Brachythecium oxycladon*, PL=*Plagiothecium micans*. Cross-hatched area=bare bark. Note relic communities of Neckera surrounded by Campylium.

3. *Anomodon attenuatus* Union. This union is by far the most characteristic and most extensive of the bryophyte unions on the deciduous trees discussed in this paper. At its maximum development, this union grows from a short distance above the six-foot-mark on the butt down to, or nearly to, the soil line. Each of the deciduous trees, save Castanea, supported a well-defined community of *Anomodon attenuatus*. On the Chestnut, the community was very local and, as the map shows (Fig. 1), grew only near the base of the tree. Two facies or sub-communities of this union occurred locally on the trunks. One facies was dominated by *Anomodon rostratus* while the other, more rare, was dominated by *Anomodon Rugelii.*

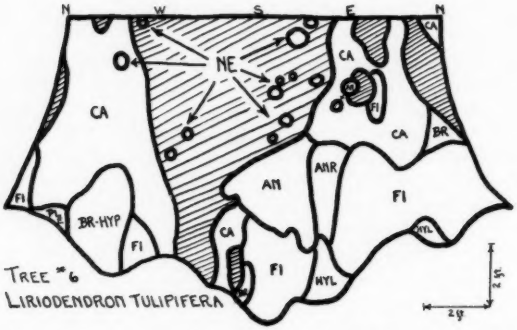

Fig. 3. Bryophytic communities on the butt of *Liriodendron tulipifera* No. 6. NE=*Neckera pennata*, CA=*Campylium chrysophyllum*, AN=*Anomodon attenuatus*, ANR *Anomodon rostratus*, FI=*Fissidens cristatus*, PLE=*Plagiothecium elegans*, BR-HYP=*Brachythecium oxycladon* and *Hypnum molluscum*, HYL=*Hylocomium brevirostre*. Cross-hatched area=bare bark.

The characteristic moss of this union, *Anomodon attenuatus*, grows in rather dense mats which makes the determination of the extent of an individual plant a difficult matter. The appearance of the Anomodon union forming a characteristic mat on *Aesculus octandra* is shown in Fig. 5. Perhaps the greatest admixture of the other species of bryophytes in this union occurs at the periphery of each community. Since the union is so extensive, it adjoins most of the other bryophyte communities present on the butt of a given tree. Thus, it is not surprising that the species list for this union is usually larger than for any other community of bryophytes on the deciduous trees. Table 2 presents the distribution data and the presence classes of the species of the *Anomodon attenuatus* union.

TABLE 2

Occurrence of the *Anomodon attenuatus* union.

Species list	Lir. 1	Lir. 4	Lir. 6	Lir. 7	Aes.	Fra.	Fag.	Cas.	Pr.
1. *Anomodon attenuatus*	x	x	x	x	x	x	x	x	5
2. *Anomodon rostratus*	x	x	x	x	x	x	x	x	5
3. *Anomodon Rugelii*	–	x	–	x	–	x	x	–	3
4. *Campylium chrysophyllum*	x	x	x	x	x	x	x	x	5
5. *Brachythecium oxycladon*	–	x	x	x	x	–	x	x	4
6. *Fissidens cristatus*	x	x	–	x	x	–	x	–	4
7. *Thuidium delicatulum*	x	x	x	–	x	–	–	x	4
8. *Radula complanata*	x	x	–	x	x	–	x	x	4
9. *Eurynchium strigosum*	–	x	–	x	–	–	–	–	2
10. *Rhodobryum roseum*	x	x	–	–	x	–	–	–	2
11. *Schwetschkeopsis dentic.*	–	–	–	–	x	–	x	–	2
12. *Forsstroemia trichomitria*	–	–	–	–	–	–	x	–	1
13. *Hylocomium brevirostre*	x	–	–	–	–	–	–	–	1
14. *Mnium affine* var. *ciliare*	–	–	–	–	–	–	–	x	1
15. *Neckera pennata*	–	–	–	–	–	–	x	–	1
16. *Metzgeria conjugata*	x	–	–	x	–	–	x	–	2

4. *Anomodon rostratus* Facies. In its floristic composition, this community is very similar to the preceding *Anomodon attenuatus* union. From this standpoint, the *Anomodon rostratus* community is better considered merely a "facies" of the more widespread union of *A. attenuatus;* but, the former community frequently grows on the bark nearer the soil line than the latter. Moreover, *Anomodon rostratus* rarely, if ever, occurs as a community much above three to four feet from the ground, whereas the *A. attenuatus* community frequently grows at or above the six-foot-mark on the butt. Thus, on the basis of habitat, the two communities are somewhat different. Table 3 records the species found in this facies and their presence classes.

TABLE 3

Occurrence of the *Anomodon rostratus* facies

Species list	Lir. 1	Lir. 4	Lir. 6	Lir. 7	Aes.	Fra.	Fag.	Cas.	Pr.
1. *Anomodon rostratus*	x	x	x	x	x	x	x	x	5
2. *Anomodon attenuatus*	x	x	x	x	x	x	x	x	5
3. *Anomodon Rugelii*	–	x	x	x	–	x	x	–	4
4. *Brachythecium oxycladon*	x	x	x	x	x	–	x	x	5
5. *Campylium chrysophyllum*	–	x	x	x	x	x	–	–	4
6. *Fissidens cristatus*	x	x	–	x	–	–	–	–	2
7. *Thuidium delicatulum*	x	x	–	x	–	–	–	–	2
8. *Hylocomium brevirostre*	x	x	–	–	–	–	–	–	2
9. *Mnium affine* var. *ciliare*	–	–	x	–	–	–	–	x	2
10. *Metzgeria conjugata*	–	x	x	–	–	–	–	–	2
11. *Hypnum molluscum*	–	–	x	–	–	–	–	–	1
12. *Radula complanata*	x	–	–	–	–	–	–	–	1

5. *Anomodon Rugelii* Facies. This facies of the Anomodon union did not appear commonly on the butts of the deciduous trees investigated. Fraxinus and Fagus were the only trees whereon the facies occurred. However, on Liriodendron, *Anomodon Rugelii* itself was often noted as a component of secondary importance within the true *Anomodon attenuatus* union.

The general region of the bark of Fraxinus and Fagus which was covered with communities of *Anomodon Rugelii* can be noted from the maps (Figs. 4 and 6). It usually grows on the upper portions of the butts between four and six feet from the ground.

The floristic composition of the facies, as it was represented on Fraxinus and Fagus, is given in the following list wherein the species are arranged in order of their estimated abundance within the community: *Anomodon Rugelii, A. attenuatus, A. rostratus, Campylium chrysophyllum, Brachythecium oxycladon, Radula complanata, Fissidens cristatus, Schwetschkeopsis denticulata,* and *Metzgeria conjugata.*

6. *Brachythecium oxycladon* Union. A Brachythecium union was observed only on two of the Liriodendrons (See maps, Figs. 2 and 3), Fagus, and Castanea. On the other deciduous trees, this moss was frequently present as a

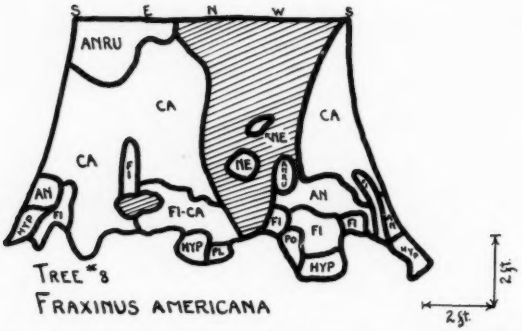

Fig. 4. Bryophytic communities on the butt of *Fraxinus americana*. NE=*Neckera pennata*, CA=*Campylium chrysophyllum*, AN=*Anomodon attenuatus*, ANRU=*Anomodon Rugelii*, HYP=*Hypnum molluscum*, FI=*Fissidens cristatus*, PL=*Plagiothecium micans*, PO=*Thamnium alleghaniense*. Cross-hatched area=bare back.

component of other bryophytic communities but did not form distinct unions. The Brachythecium union grows near the soil line of the foregoing species of trees and is never characteristic of the upper regions of the butts. Because of the frequent proximity of this union to the soil line, it may include a number of mosses which are not truly corticolous. For example, such mosses as *Rhodobryum roseum, Plagiothecium micans,* and *Thamnium alleghaniense* occasionally become members of an epiphytic bryophyte community where the bark may have become impregnated locally with sufficient soil particles.

The most important components of the *Brachythecium oxycladon* union on the deciduous trees are, besides Brachythecium itself, *Anomodon attenuatus, Campylium chrysophyllum, Fissidens cristatus, Thuidium delicatulum, Anomodon rostratus, Hylocomium brevirostre, Hypnum molluscum, Entodon seductrix, Eurhynchium strigosum,* and *Anomodon Rugelii.*

7. *Thuidium delicatulum* Union. The *Thuidium delicatulum* union grows on approximately the same region of the bark of deciduous trees as that of Brachythecium. On Liriodendron, especially, Thuidium often covers the tops of the larger roots and merges distally with various non-corticolous bryophytes. Besides occurring on Liriodendron, this union also grows on Castanea and Tsuga. (See maps, Figs. 1 and 7). The different species of which this union is composed are given in Table 5 in order to bring out a comparison of the community on deciduous trees with that on Tsuga.

8. *Fissidens cristatus* Union. This community reaches perhaps its maximum development on Liriodendron (map, Fig. 3), but it also occurs on the bark of Fraxinus and Fagus (maps, Figs. 4 and 6). In general, a Fissidens union is most often developed on the bark of these trees at, or near, the soil line, thus sharing that region of the tree-butt with communities of Thuidium, Brachythecium, and even Hylocomium. On Liriodendron, a Fissidens union

may grow well up on the trunk if habitat conditions there are especially favorable (See map, Fig. 3).

The most important species of bryophytes of the *Fissidens cristatus* union, arranged in order of relative abundance within the community, are *Fissidens cristatus, Anomodon attenuatus, A. rostratus, Eurhynchium strigosum, Campylium chrysophyllum, Brachythecium oxycladon, Thuidium delicatulum, Metzgeria conjugata, Hypnum molluscum, Dicranum scoparium, Hylocomium brevirostre, Rhodobryum roseum, Mnium affine* var. *ciliare,* and *Plagiothecium micans.*

9. *Hylocomium brevirostre* Union. Although the Hylocomium union may grow on the bark of the deciduous trees up to a height of two to three feet from the ground, it is more characteristic of the base of the butts and on the tops of the roots. Where a Thuidium community occurs on the top of a root,

Fig. 5. Typical *Anomodon attenuatus* mat on *Aesculus octandra.* The butt of this tree was mapped and designated as tree No. 2.

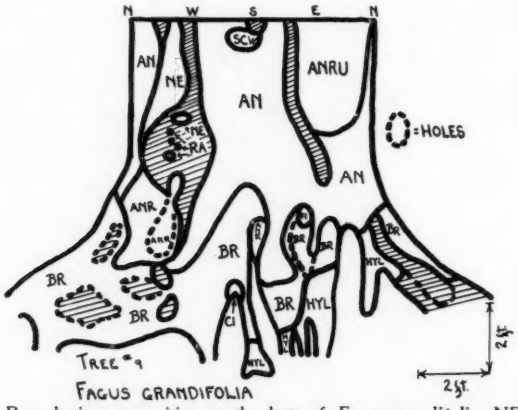

Fig. 6. Bryophytic communities on the butt of *Fagus grandifolia*. NE=*Neckera pennata*, RA=*Radula complanata*, AN=*Anomodon attenuatus*, ANR=*Anomodon rostratus*, ANRU=*Anomodon Rugelii*, SCW=*Schwetschkeopsis denticulata*, BR=*Brachythecium oxycladon*, CI=*Cirriphyllum Boscii*, HYL=*Hylocomium brevirostre*, FI=*Fissidens cristatus*. Cross-hatched area=bare bark.

Hylocomium may also grow, especially on the distal extremities. Among the deciduous trees investigated, only the Liriodendrons and Fagus supported a Hylocomium union. The bryophyte community reaches its maximum epiphytic development on Liriodendron where it may have a rather high coverage (See map, Fig. 2). Since a Hylocomium union also occurs on Tsuga, a consideration of the floristic composition of the community is deferred until the various epiphytic bryophytes on Hemlock have been described.

10. *Hypnum molluscum Union*. A distinct union of *Hypnum molluscum* was observed only on Fraxinus and Liriodendron. On these trees, this bryophyte community grew in much the same region of the butt as the Hylocomium union. The coverage of this community on any given tree, in so far as our studies indicated, was very low. In one instance, *Hypnum molluscum* grew in about equal abundance with *Brachythecium oxycladon* and the community has been designated as a "joint" union of these two mosses (See map, Fig. 3). Since the species found in the "joint" union of Hypnum and Brachythecium were virtually the same as in the true *Hypnum molluscum* union, merely the porportions of the two dominant mosses being altered, a separate description of this community does not seem necessary.

Cain and Sharp (1938) group all Hypnum communities into one union with several facies dominated by individual species. It seems logical to designate such a community of *Hypnum molluscum*, as occurs on deciduous trees, as a separate union because of the species of bryophytes of which it is made up and because of its habitat. Its characteristic mosses are those of other deciduous tree unions and its presence on the bark of the deciduous trees

marks it as having different ecological requirements than the Hypnum communities on Tsuga.

The important species included within the *Hypnum molluscum* union are, besides Hypnum, *Eurhynchium strigosum, Plagiothecium micans, Brachythecium oxycladon, Anomodon rostratus, Campylium chrysophyllum, Hylocomium brevirostre, Thuidium delicatulum,* and *Fissidens cristatus.*

11. *Eurhynchium strigosum* Union. Though of small coverage on the butt of the tree as a whole, this union of Eurhynchium nevertheless deserves recognition since it is rather well-marked in species composition and in its habitat. The characteristic habitats of the Eurhynchium community are on the bark surrounding a cavity in the tree, or on the shaded sides of the roots or, in some instances, at the soil line where conditions are favorable (See map, Fig. 2). The Eurhynchium community was observed only on Liriodendron, but the moss itself frequently grew in other communities upon most of the other deciduous trees considered in this paper.

The important species found in the *Eurhynchium strigosum* union are, besides the dominant moss, *Brachythecium oxycladon, Plagiothecium micans, Anomodon attenuatus, A. rostratus, Fissidens cristatus,* and *Campylium chrysophyllum.*

12. Miscellaneous communities. Local and very restricted communities of such mosses as *Thamnium alleghaniense, Cirriphyllum Boscii,* and *Mnium affine* var. *ciliare* which are not typically corticolous are sometimes met with at the bases of the deciduous trees, but they do not appear to be important enough as epiphytic vegetation to be treated here in detail.

II. BRYOPHYTE UNIONS ON *Tsuga canadensis*

1. *Ulota crispa* Union. Like the *Neckera pennata* union on the deciduous species of trees, the Ulota community grows on the bare bark. On most Hemlocks, Ulota is very infrequent below the crown and upper trunk communities where it is the principal bryophyte represented. Thus, a detailed study of a recently wind-thrown Tsuga over one hundred and twenty feet in height indicated that Ulota is most characteristic of the upper trunk and especially the crown communities. The occurrence of this union on the butt or lower six feet of the tree did not appear to be common except where physiographic conditions were especially favorable. On the Tsuga trunks investigated, Ulota grew on the butt only where the tree was adjacent to a mountain stream. The *Ulota crispa* union, as it occurred on the butt, consisted only of that moss. (See map, Fig. 7).

2. *Dicranum fulvum-Bazzania denudata* Union. Both components of this "joint" union may grow separately on the bare bark of the Tsuga butt, although from the accompanying map (Fig. 7) of the epiphytic bryophytes on the tree, it will be noted that Dicranum and Bazzania may form a community wherein each is of about equal importance. The union was developed on only one of the Tsuga trunks investigated, though each of these bryophytes also grew in another community on the tree.

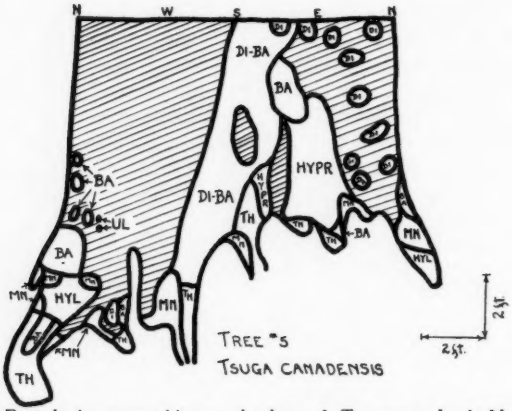

Fig. 7. Bryophytic communities on the butt of *Tsuga canadensis* No. 5. BA=*Bazzania trilobata*, DI=*Dicranum fulvum*, DI-BA=*Dicranum fulvum* and *Bazzania denudata*, HYPR=*Hypnum reptile*, MN=*Mnium hornum*, HYL=*Hylocomium brevirostre*, TH=*Thuidium delicatulum*, UL=*Ulota crispa*. Cross-hatched area=bare bark.

The principal bryophytes of the union are *Dicranum fulvum, Bazzania denudata, Hypnum reptile, Thuidium delicatulum,* and *Mnium hornum.*

3. *Hypnum reptile* Union. On Hemlocks in comparatively dry situations, the *Hypnum reptile* union appears to be of the highest coverage on the bark of the butt. As a matter of fact, this union was the only one developed on the first Tsuga studied. On the second Hemlock, that near a stream, the Hypnum union was somewhat reduced as far as coverage of the butt as a whole was concerned, but its floristic composition was fundamentally similar, save for an abundance of leafy liverworts, to that on the first tree. This union may well be only a facies of the collective Hypnum union of Cain and Sharp (1938).

The important epiphytic mosses of the Hypnum union are *Hypnum reptile, Dicranum fulvum, Brotherella recurvans, Thuidium delicatulum,* and *Sematophyllum microcarpon.* On the second Tsuga, there also grew in this union *Brachythecium oxycladon, Sematophyllum marylandicum,* and several liverworts, including *Frullania Asagrayana, Microlejeunea ulicina, Lepidozia sylvatica, L. reptans, Blepharostoma trichophyllum,* and *Sphenolobus exsectus.* Of all the above bryophytes, those which are most important, as far as coverage within each example of the union is concerned, are the mosses *Hypnum reptile, Dicranum fulvum, Brotherella recurvans,* and *Thuidium delicatulum.*

4. The remaining communities on Tsuga, those of *Bazzania trilobata, Hylocomium brevirostre, Mnium hornum,* and *Thuidium delicatulum,* occurred only on one tree near the stream and were principally developed on the tops of several large roots.

The *Bazzania trilobata* community, which Cain and Sharp (1938) consider a facies of their Hypnum union, grew almost exclusively on the tops of large roots. Besides *Bazzania trilobata,* the community includes *Dicranum fulvum, Hypnum reptile, Thuidium delicatulum, Hylocomium brevirostre,* and *Mnium hornum.*

The *Mnium hornum* union which grew at the base of the tree, and also on the roots, was composed of *Bartramia pomiformis, Bazzania trilobata, Catharinea undulata, Brotherella recurvans, Dicranum fulvum, Hylocomium brevirostre,* and *Thuidium delicatulum.*

The *Hylocomium brevirostre* and *Thuidium delicatulum* communities on the base of Tsuga differed somewhat from the unions of the same name on the bark of the deciduous trees. A comparison of the two unions on the two different types of trees is of interest, because it indicates that, under optimum conditions, some of the same bryophytic communities that occur on deciduous trees may also develop on Tsuga. A tabular comparison of these two unions on the two types of trees follows in Tables 4 and 5.

From the table of the Hylocomium union, it is significant that the most important mosses of the community, those of high presence and of high coverage, are very nearly identical on the two types of trees. Of the mosses of low presence and coverage, *Anomodon attenuatus, A. rostratus, Campylium chrysophyllum,* and *Eurhynchium strigosum* are exclusive to the Hylocomium union of the deciduous trees and are not found in Tsuga. On the other hand, *Dicranum fulvum, Hypnum reptile,* and *Mnium hornum,* which are of low presence and coverage also, are exclusive to the Hylocomium community of Tsuga. With the exception of these mutually exclusive species of bryophytes of low presence and coverage, the Hylocomium union is very much the same on the two contrasted types of trees.

TABLE 4

Occurrence of the *Hylocomium brevirostre* union.

Species list	Lir. 1	Lir. 4	Lir. 6	Lir. 7	Fag.	Tsu.	Pr.
1. *Hylocomium brevirostre*	x	x	x	x	x	x	5
2. *Brachythecium oxycladon*	x	x	x	x	x	–	5
3. *Fissidens cristatus*	x	–	x	x	x	x	5
4. *Thuidium delicatulum*	x	x	–	–	x	x	4
5. *Anomodon attenuatus*	x	–	–	–	x	–	2
6. *Anomodon rostratus*	–	x	x	–	–	–	2
7. *Campylium chrysophyllum*	–	–	–	x	x	–	2
8. *Eurhynchium strigosum*	x	–	–	x	–	–	2
9. *Dicranum fulvum*	–	–	–	–	–	x	1
10. *Hypnum reptile*	–	–	–	–	–	x	1
11. *Hypnum imponens*	–	–	–	–	–	x	1
12. *Mnium hornum*	–	–	–	–	–	x	1
13. *Brotherella recurvans*	–	–	–	x	–	–	1
14. *Hypnum molluscum*	–	–	–	x	–	–	1
15. *Plagiothecium elegans*	–	–	–	x	–	–	1
16. *Rhodobryum roseum*	x	–	–	–	–	–	1
17. *Cephalozia curvifolia*	–	–	–	–	–	x	1

TABLE 5

Occurrence of the *Thuidium delicatulum* union.

Species list	Lir. 1	Lir. 4	Lir. 7	Cas.	Tsu.	Pr.
1. *Thuidium delicatulum*	x	x	x	x	x	5
2. *Anomodon attenuatus*	x	–	x	x	–	3
3. *Brotherella recurvans*	–	x	–	x	x	3
4. *Hylocomium brevirostre*	–	x	–	x	x	3
5. *Anomodon rostratus*	x	x	–	–	–	2
6. *Brachythecium oxycladon*	x	x	–	–	–	2
7. *Campylium chrysophyllum*	–	–	x	–	x	2
8. *Eurhynchium strigosum*	x	–	x	–	–	2
9. *Fissidens cristatus*	–	x	–	x	–	2
10. *Mnium affine* var. *ciliare*	–	x	x	–	–	2
11. *Rhodobryum roseum*	x	x	–	–	–	2
12. *Hypnum imponens*	–	–	–	–	x	1
13. *Hylocomium splendens*	–	–	–	–	x	1
14. *Plagiothecium elegans*	–	–	x	–	–	1
15. *Schwetschkeopsis dentic.*	–	–	x	–	–	1
16. *Cephalozia curvifolia*	–	–	–	–	x	1

Furthermore, a comparison of the *Thuidium delicatulum* union on the deciduous trees with that on Hemlock brings out the point, just set forth for the Hylocomium community, that the important species of high presence classes and of high coverage in the union are mostly present on both types of trees. From Table 5, it will be noted that, with the exception of *Anomodon attenuatus, A. rostratus,* and *Brachythecium oxycladon,* the important species shared in the Thuidium union on both types of trees are *Thuidium delicatulum, Brotherella recurvans, Hylocomium brevirostre,* and *Campylium chrysophyllum. Plagiothecium elegans* and *Schwetschkeopsis denticulata,* mosses of low presence and coverage in this union, appear to be exclusive to the deciduous trees, and, on the other hand, *Hylocomium splendens* and *Hypnum imponens* are confined to Tsuga. Thus, aside from individual indicator species characteristic of each type of tree, the Thuidium union, like that of Hylocomium, is fundamentally the same for both Tsuga and the deciduous trees.

List of the bryophytes collected and identified in this study.

A. Musci

1. *Anomodon attenuatus*
2. *Anomodon rostratus*
3. *Anomodon Rugelii*
4. *Brachythecium oxycladon*
5. *Brotherella recurvans*
6. *Bartramia pomiformis*
7. *Campylium chrysophyllum*
8. *Catharinea undulata*
9. *Cirriphyllum Boscii*
10. *Dicranum fulvum*
11. *Dicranum scoparium*
12. *Entodon seductrix*
13. *Eurhynchium serrulatum*
14. *Eurhynchium strigosum*
15. *Fissidens cristatus*
16. *Forsstroemia trichomitria*
17. *Georgia pellucida*
18. *Homalotheciella subcappillata*
19. *Hylocomium brevirostre*
20. *Hylocomium splendens*
21. *Hypnum imponens*
22. *Hypnum molluscum*
23. *Hypnum reptile*
24. *Mnium affine* var. *ciliare*
25. *Mnium hornum*
26. *Neckera pennata*
27. *Plagiothecium elegans*
28. *Plagiothecium micans*
29. *Plagiothecium Muellerianum*
30. *Polytrichum ohioense* (?)
31. *Raphodostegium adnatum*
32. *Rhodobryum roseum*
33. *Schwetschkeopsis denticulata*
34. *Sematophyllum marylandicum*
35. *Sematophyllum microcarpon*
36. *Thamnium alleghaniense*
37. *Thuidium delicatulum*
38. *Ulota crispa*

B. Hepaticae

1. *Bazzania denudata*
2. *Bazzania trilobata*
3. *Blepharostoma trichophyllum*
4. *Cephalozia curvifolia*
5. *Frullania Asagrayana*
6. *Frullania Brittoniae*
7. *Lepidozia reptans*
8. *Lepidozia sylvatica*
9. *Metzgeria conjugata*
10. *Microlejeunea ulicina*
11. *Radula complanata*
12. *Scapania nemorosa*
13. *Sphenolobus exsectus*

A total of 51 species of bryophytes, collected from the barks of the various trees studied in this problem, were identified. The nomenclature generally followed is that of Sharp (1938).

B. Bark Factors

The results of the study of the bark factors appear in Tables 6 to 11 and in Figs. 8 to 11. The tables illustrate the results shown by the field moisture and hydrogen-ion studies while the graphs portray the results of the experiments on the rate of drying-out and the rate of moisture absorption of the bark.

FIELD MOISTURE

The field moisture data, showing the amounts of water in the bark of different tree species at comparable levels at the same time, exhibit some surprising facts. These data are presented in Tables 6 to 8, each table including samples collected at the same time and, therefore, comparable. The results from Tree No. 10, a Castanea, do not appear in these tables because they were collected at a different time than any of the other samples and so cannot be compared. As far as the altitudinal location on the tree is concerned, however, they are like the other samples and show similar trends of vertical distribution of bark moisture.

Samples from a Liriodendron, an Aesculus, and a Tsuga were collected on October 25, 1936. The bark of all of these trees showed a decided gradient from a high moisture content under moss cover at three feet to a low moisture content of the bare bark at six feet. On the north side of the Liriodendron, there was almost six times as much water in the bark under the moss at three feet as was present in the bare bark at six feet. This great difference in moisture content between bare bark and moss-covered bark may

Table 6

Field moisture content of bark on October 25, 1936. (Average percentages)

Location on tree	Tree 1 Liriodendron	Tree 2 Aesculus	Tree 3 Tsuga
N side, under moss, 3 ft.	168.6	69.0	22.6*
N side, moss margin, 4-5 ft.	94.6	49.4	
N side, bare bark, 6 ft.	28.8	32.6	21.1
S side, under moss, 3 ft.	181.9	88.7	64.8
S side, moss margin, 4-5 ft.	106.6	89.4	
S side, bare bark, 6 ft.	60.3	35.6	29.3

* bare bark.

be due partly to decreased evaporation and run-off caused by the bryophyte mat as well as to differences in bark characteristics. In all three cases, the bark on the south side of the tree was more moist than that on the north. This may have been caused by a recent rain falling from that direction. In almost all of the trees studied, most of the bryophyte cover was found to occur on the south or east face of the trunk; this may indicate that most of the rains are blown against the tree from these directions. The south sides of the trunks face the ridge bounding the watershed and the east sides face toward the upper end of the Ramsey valley and the high main ridge of the Smokies. Thus, these two sides are exposed to the moisture-laden downdraft of cold air from the higher altitudes and receive a great deal of moisture that is blown against them. Richards (1932) says, "Wind profoundly affects moss vegetation. Its effects are particularly obvious on epiphytes. In England the trees are usually moss-grown only on the western and south-western sides (which face the prevailing wind). This effect is probably due to the rain being driven against the tree trunks." Olsen (1917) and Wilson (1936) both found that the upper sides of leaning trees supported more luxurious epiphytic bryophyte vegetation due to the catching of falling rain.

Comparing the relative amounts of water in the bark of the three different species of trees, it can be seen that the Liriodendron bark was much more moist than that of either the Aesculus or the Tsuga. At the three-foot-level, the bark of Liriodendron contained approximately twice as much water as did that of Aesculus at the same level, and from three to seven times as much as the bark of Tsuga at the same height. The proportions decrease with increase in height but, on the whole, Liriodendron bark appears to hold much more water under similar conditions than that of Aesculus or Tsuga. The latter two have rather hard, impermeable barks as compared to the more soft, sponge-like bark of the mature Liriodendron. These results were substantiated when comparing Tree No. 5, a Tsuga, with two other Liriodendrons, as brought out in Table 7. Fraxinus and Fagus were also found to have barks which were more dry than that of Liriodendron. Samples from trees of each of these genera were collected on November 8, 1936. The weather was damp and rain had fallen recently, so that the samples were rather high in moisture content. Fraxinus, according to these results, stood intermediate between Liriodendron and Fagus in regard to the amount of water present in the bark. The bark of Fagus, at the levels under six feet, contained only about

TABLE 7

Field moisture content of bark on November 1, 1936. (Average percentages)

Location on tree	Tree 4 Liriodendron	Tree 5 Tsuga	Tree 6 Liriodendron
N side, under moss, 3 ft.	145.5	32.0	161.3
N side, moss margin, 4-5 ft.	118.9		58.0
N side, bare bark, 6 ft.	111.1	22.9	34.1
S side, under moss, 3 ft.	139.1	68.3	168.3
S side, moss margin, 4-5 ft.			84.8
S side, bare bark, 6 ft.	124.8*	23.8	27.4

* moss margin.

half as much moisture as that of Liriodendron at similar heights. This is readily explained by the hard, more or less impermeable bark of the Fagus. It is possible that if the bark of the Fagus had been collected at a time when the atmosphere was more dry, it would approach that of Tsuga in the amount of moisture held. Tabular comparison of the bark moisture of these three species is presented in Table 8.

TABLE 8

Field moisture content of bark on November 8, 1936. (Average percentages)

Location on tree	Tree 7 Liriodendron	Tree 8 Fraxinus	Tree 9 Fagus
N side, under moss, 3 ft.	187.0	116.6*	96.4
N side, moss margin, 4-5 ft.	160.9	134.0@	73.5*
N side, bare bark, 6 ft.	90.1	50.4	64.3@
S side, under moss, 3 ft.	203.5	155.0	81.5
S side, moss margin, 4-5 ft.	147.5	145.6	77.9
S side, bare bark, 6 ft.	90.9	100.8	86.2

* bare bark. @ Neckera margin.

The effect of height and exposure on the moisture content of the bark is clearly shown in Tables 9 and 10. These are the results of two series of field moisture samples taken from Tree No. 6, a Liriodendron, on March 21, 1937. The first series was taken on the southeast face of the trunk, at intervals of

TABLE 9

Field moisture content of bark on March 21, 1937.
Tree 6, Liriodendron. Vertical series. Southeast face.

Height	Union	Percentage Water
Base	Hylocomium	182.5
.5 ft.	Fissidens	202.8
1.0 ft.	Fissidens	186.4
1.5 ft.	Anomodon rostratus	205.0
2.0 ft.	Anomodon rostratus	168.9
2.5 ft.	Campylium	135.0
3.0 ft.	Campylium	120.3
3.5 ft.	Campylium	99.2
4.0 ft.	Bare bark	66.6
4.5 ft.	Bare bark and Campylium	37.0
5.0 ft.	Neckera and Bare bark	27.9
5.5 ft.	Neckera and Bare bark	27.7
6.0 ft.	Bare bark	25.9

six inches, from the ground level to a height of six feet. This series brings out again, in a convincing manner, the definite gradation from the very moist bark near the base of the butt to the dry bark above five feet. The bark below two feet and under the cover of the bryophytes was approximately eight times as moist as the bare bark above five feet bearing patches of Neckera. It is interesting to note the definite zonation of the bryophyte communities as shown on this tree. Near the base, on bark with high water content, were the communities of *Hylocomium brevirostre*, *Fissidens cristatus*, and *Ano-*

modon rostratus. Then, on bark with an intermediate amount of moisture, were broad patches of the Campylium union. Above five feet, on the very dry bark, were scattered patches of Neckera.

TABLE 10

Field moisture content of bark on March 21, 1937.
Tree No. 6, Liriodendron. Horizontal series. Height of 3 feet.

Exposure	Union	Percentage Water
South-southeast	Anomodon attenuatus	161.1
Southeast	Fissidens	168.3
East	Fissidens	203.4
East-northeast	Brachythecium	153.4
Northeast	Brachythecium	185.0
North	Fissidens	181.0
North-northwest	Campylium	138.2
Northwest	Campylium	151.1
West-northwest	Campylium	117.9
West	Neckera and Bare bark	38.9
West-southwest	Bare bark	38.4
Southwest	Bare bark	38.7
South	Neckera	114.6

The second series on Tree No. 6, showing the effect of exposure on the field moisture content of the bark, was taken at intervals of one foot at a height of three feet all around the trunk. The bark on the east face of the trunk contained the most moisture. The driest face of the trunk was the southwest exposure, where the bark contained about one-fifth of the amount of moisture present in the bark on the east side of the trunk. The north and south faces were intermediate in the amount of water present in the bark, with the north side somewhat more moist than the south. The abundant moisture on the east side of the trunk seems to bear out Richards' (1932) theory that luxuriant bryophyte growth on the side toward the prevailing wind is the result of rain being driven against the trunk. It is from this direction (east) that the moist down-drafts of cold air from the higher altitudes flow in the Ramsey valley. The east and the northeast faces are covered with the Fissidens and the Brachythecium unions, while the northwest is occupied by Campylium and the west and southwest by isolated patches of Neckera. The south exposure bears some Neckera and a patch of the *Anomodon attenuatus* union which adjoins a portion of the Fissidens union on the southeast.

WATER-HOLDING CAPACITY AND RATE OF DRYING-OUT

The experiments on the water-holding capacity and the rate of drying-out of the bark reveal some interesting facts. In the first series of these experiments, bark from a Liriodendron was compared with that of Aesculus and Fraxinus. These results are graphically portrayed in Fig. 8. In this graph, the average of six samples taken from representative parts of the butt region is used as the value for the species. Of these three species, Liriodendron had

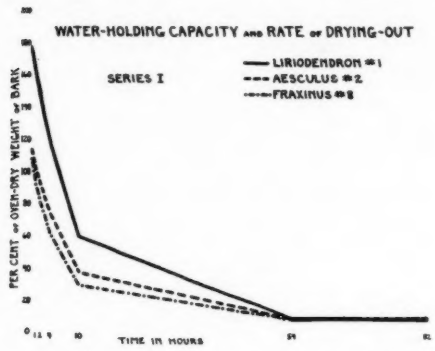

Fig. 8. Water-holding capacity and the rate of drying-out of the bark of *Liriodendron tulipifera* No. 1, *Aesculus octandra*, and *Fraxinus americana*. The values were obtained from an average of six bark samples from representative parts of the butt region of each tree.

by far the highest water-holding capacity, holding an average of 178 per cent moisture on an oven-dry weight basis when fully saturated, or almost twice as much water as the weight of the bark itself. The bark of the Aesculus held 114.3 per cent of its oven-dry weight in moisture when completely soaked and that of the Fraxinus held 109.2 per cent. The rate of drying-out, as might be expected, was most rapid in the first few hours after exposure to the air. In the first hour, the percentage of water held in the Liriodendron bark fell from 178 per cent to 160.4 per cent; that of Aesculus from 114.3 per cent to 102.3; and that of Fraxinus from 109.2 to 93.3 per cent. In other words, the bark of these three species lost an average of a little over 10 per cent of the water in the space of one hour. After 10 hours, the bark of the Liriodendron held only 59.7 per cent of its weight in moisture, while the Aesculus and the Fraxinus held 37.4 and 29.6 per cent, respectively. The Liriodendron and the Aesculus lost roughly two-thirds of the total amount of water in 10 hours and the Fraxinus lost as much as three-quarters of its total amount in the same length of time. About this time, the rate of drying-out began to slow down and at the end of 54 hours the samples had reached an almost constant air-dry weight. At this time, the bark from all three of the trees contained approximately 9 per cent water on an oven-dry weight basis. Thus, this experiment shows that while Liriodendron bark will hold a much greater amount of water than the barks of Aesculus and Fraxinus, the rate of drying-out is nearly the same. However, the bark of Liriodendron at all times, until completely air-dry, contains more water than those of the other two species.

The results of the second series of drying-out experiments are shown in Fig. 9. The values in this graph also represent the average of six samples taken from various parts of the butt region of the tree. In this series, Liriodendron was again used as a standard against which the other species were

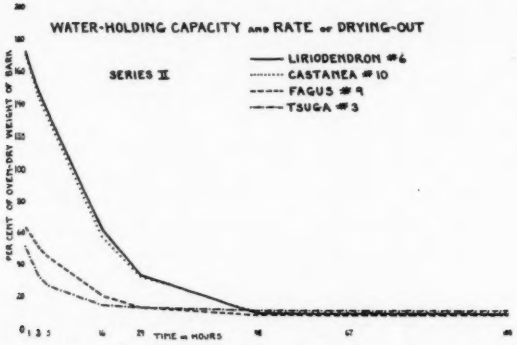

Fig. 9. Water-holding capacity and the rate of drying-out of the bark of *Liriodendron tulipifera* No. 6, *Castanea dentata*, *Fagus grandifolia*, and *Tsuga canadensis* No. 3. Values represent averages of six bark samples from each tree.

compared. Liriodendron No. 6 was the specific tree used in this instance. Castanea, Fagus, and Tsuga were the other trees used in this set of experiments. The bark of the Liriodendron again showed the highest water-holding capacity with 172.9 per cent, although that of Castanea with 170.1 per cent was almost the same. The barks of Fagus and Tsuga showed the lowest water-holding capacities of any of the barks investigated with percentages of 63.8 and 51.6 respectively. This is in strong contrast to the capacities of Liriodendron and Castanea which held almost twice their oven-dry weight in water when completely saturated. As in the previous experiment, the rate of drying-out was greatest in the first few hours after the samples were removed from the water. After 24 hours, there was a gradual decrease in the speed of drying-out and an almost constant air-dry weight was reached in 48 hours. The bark of the Tsuga, however, had practically reached its air-dry weight in the short space of 16 hours. When air-dry, it held more water than the bark of any other species. The amounts of water held in the barks of the other species when air-dry were about the same as that held by the other kinds of bark in the previous experiment. This value was around 9 per cent of the oven-dry weight of the bark; the bark of Tsuga held almost 11 per cent moisture when air-dry. The barks of Castanea and Liriodendron proved to be very similar as regards both the water-holding capacity and the rate of drying-out and seldom varied more than 2 or 3 per cent in the amount of moisture present at any time during the experiment. The outstanding fact brought to light by this series was the great difference in the amounts of water held by the different barks. Those of Fagus and Tsuga held only about half their oven-dry weights in moisture while Liriodendron and Castanea held almost twice their oven-dry weights. Considerable amounts of water remained in the barks of the latter two species of trees after those of the Tsuga and Fagus had become air-dry, since it took the bark of Liriodendron and Castanea from two to three times as long to reach the air-dry condition. No significant

differences were noted in the water-holding capacity and rate of drying-out of the bark from different locations on the same tree. On one or two trees, however, the lower bark held much more moisture when completely saturated than the bark which was obtained at a height of six feet. This was especially noticeable in Liriodendron and Castanea but was negligible or absent in the bark of the other species. This difference may have been due to the effect of bryophyte communities or to natural changes in the bark.

RATE OF ABSORPTION FROM A SATURATED ATMOSPHERE

Since the Ramsey valley is very often filled with fog, two series of experiments to investigate the absorption of water by the bark from a saturated atmosphere were set up. The results of these two series appear in Figs. 10 and 11. The first series consisted of the same samples that were used in the first set of drying-out experiments, namely those from Liriodendron, Aesculus, and Fraxinus. The temperature of the moist chamber was 6 degrees Centigrade maintained fairly constantly in an electric refrigerator. The rate of absorption at this temperature was most rapid during the first 24 hours. The Liriodendron bark absorbed 16.2 per cent of its oven-dry weight in this length of time, while that of Aesculus absorbed 13.5 per cent of its oven-dry weight in water, and that of the Fraxinus 13.7 per cent. From this point, there was gradually diminishing absorption and at the end of 168 hours, Liriodendron held 25.1 per cent, Aesculus held 23.9 per cent, and Fraxinus held 21.3 per cent. Thus, in absorption of water from the atmosphere, the three barks stand in the same relation to each other as they do in water-holding capacity and rate of drying-out. The bark of Liriodendron holds the most water when saturated, holds more over a longer period of time, and absorbs the most from the atmosphere. The other two, Aesculus and Fraxinus follow in that order in all three cases. When these results on absorption are studied along with the results of the drying-out experiments, it can be seen that foggy nights or a foggy day in every two or three will keep the bark more moist than a hard rain once a week.

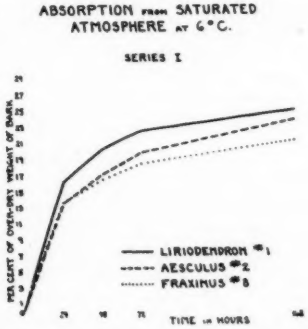

Fig. 10. Absorption of water from saturated atmosphere at 6° C. Values obtained with same series of bark samples used in the drying-out experiment illustrated in Fig. 8.

The second series of these experiments, using the same samples as the second set of drying-out experiments, bears out the above results on speed and amount of absorption. In this series, at the end of 168 hours, the bark of Liriodendron had taken in 23.2 per cent of its oven-dry weight in water; that of Castanea, 23.1 per cent; that of Tsuga, 18.0 per cent; and that of Fagus, 16.6 per cent. This is almost the same order in which these barks held water when fully saturated. Liriodendron and Castanea had barks very much alike in holding water and in the amounts held at various times during drying-out and they are very much alike in the amounts absorbed from the

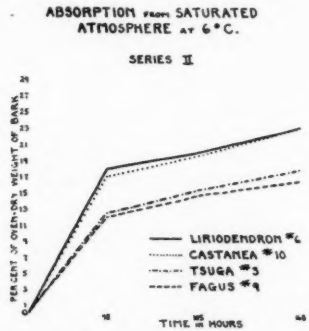

Fig. 11. Absorption of water from saturated atmosphere at 6° C. Values obtained with the same series of bark samples used in the drying-out experiment illustrated in Fig. 9.

atmosphere. Fagus and Tsuga, as would be expected from the other results, did not absorb nearly as much as did Liriodendron and Castanea. However, the bark of Tsuga which did not hold as much water when fully saturated as that of Fagus, absorbed more water than the latter from the saturated atmosphere. No significant differences were noted in the absorption of water from the air by the bark at different heights or exposures on the butt region.

HYDROGEN-ION CONCENTRATION

The pH values of the bark of the various species of trees are recorded in Table 11. The bark of all of the species was quite acid, ranging principally between pH 6.0 and pH 5.0. Practically the only values more acid than pH 5.0 were those of Tsuga. The bark of this species ranged between pH 4.96 and pH 4.28. All of the other species were somewhat alike in their reaction and were less acid than Tsuga. Of these, Aesculus was the closest to the alkaline side with values ranging between pH 6.04 and pH 5.67. No differences of consequence were noted in the reactions of the bark from different locations on the butt. The principal difference in the barks, as regards H-ion concentration, seems to be the slightly greater acidity of the bark of Tsuga as contrasted to that of the other species. This may be part of the explanation of the different moss flora present on that tree.

TABLE 11

Hydrogen-ion concentration of the bark (electrometric method).

Tree	3 ft. under moss	4-5 ft. moss margin	6 ft. bare bark
1 Liriodendron	5.89, 5.67	5.40, 5.86	5.64, 5.72
2 Aesculus	5.86, 5.67	5.89, 5.72	6.04, 6.01
3 Tsuga	4.79, 4.96*		4.54, 4.43
4 Liriodendron	5.75, 5.28	5.43	5.20, 5.26
5 Tsuga	4.54, 4.33		4.43, 4.28
6 Liriodendron	5.30, 5.20	5.77, 5.43	5.67, 5.30
7 Liriodendron	5.21, 4.81	5.11, 4.91	5.35, 5.40
8 Fraxinus	5.18,* 5.13	5.23, 5.13	5.27, 5.25
9 Fagus	5.37, 4.91	5.84,* 5.52	5.85, 5.26
10 Castanea	5.48, 5.35@	5.35,* 5.48	5.45, 5.38

* bare bark. @ moss margin.

Discussion and Integration

The results of this investigation of corticolous bryophyte communities have shown that there are marked differences in the types and compositions of these communities as they occur on several species of trees. The most striking differences separate the bryophyte unions on the trunks of deciduous trees from those on the trunks of Tsuga, a conifer. Communities of *Neckera pennata, Anomodon attenuatus,* and *Anomodon rostratus* were present on every individual deciduous tree studied and not one example of these was found on the bark of Tsuga. In addition, important unions such as those of *Campylium chrysophyllum, Brachythecium oxycladon,* and *Fissidens cristatus,* while not present on every deciduous individual, were confined to this type of tree and were absent from Tsuga. On the other hand, communities of *Ulota crispa, Dicranum fulvum-Bazzania denudata, Hypnum reptile, Bazzania trilobata,* and *Mnium hornum* were exclusive to the bark of Tsuga. This dissimilarity of corticolous bryophytic flora cannot be explained by any factor of the macro-habitat. All of the trees studied were in the same physiographic location and in similar surroundings. In some cases the trees were almost side by side. The factors of the macro-habitat being equal, the cause of the differences lies in the factors of the micro-habitat. Light, temperature, humidity, and wind were more or less of the same intensity at the same place on all of the trees due to their location in the same topographic area and their proximity to each other. The two important factors which could have differed in the micro-habitats were the character of the bark and the amount of moisture present in or on the bark. Of these two, the moisture content would have been largely dependent on variations in bark characteristics for any differences among the several trees.

Our investigations show that almost all of the deciduous trees, with the exception of Fagus, have a much softer and more sponge-like bark than that of Tsuga. In field condition, these Angiosperm barks were found to contain from two to seven times as much moisture as that of Tsuga, depending on

the species and height of bark on the trunk. This is the result of the impervious nature of the Tsuga bark. Laboratory experiments showed that the bark of Tsuga would hold only about half of its oven-dry weight in water when fully saturated, while that of Liriodendron and that of Castanea held almost twice their oven-dry weights in water under the same conditions. When allowed to dry-out, the bark of Tsuga reached a stable air-dry condition in 16 hours or one-third of the time taken by those of Liriodendron and Castanea to reach a similar state. The only deciduous tree to approach Tsuga in the low water-holding capacity of its bark and the speed of bark drying-out was Fagus, whose bark was similar in texture. Even the bark of Fagus was capable of holding considerably more moisture over a longer period of time than that of the conifer. In the absorption of water from a saturated atmosphere, the bark of Tsuga took in less moisture than any other bark except that of Fagus. The bark of Tsuga absorbed 18 per cent of its oven-dry weight while that of Fagus took in 16.6 per cent. As far as living bryophytes are concerned, however, there was more available water in the Fagus bark since it contained but 8 per cent moisture when air-dry whereas that of Tsuga contained almost 11 per cent when in the air-dry condition. Everything considered, the bark of Tsuga is markedly drier than any of the other barks studied. The bark capable of holding the greatest amounts of water over the longest periods of time are those of Liriodendron and Castanea, followed by Aesculus, Fraxinus, and Fagus, in that order.

As regards the hydrogen-ion concentration in the various barks, that of Tsuga was the most acid, ranging from pH 4.28 to pH 4.96. The other barks were slightly less acid, ranging mostly between pH 5. and pH 6.

Bark characteristics influencing corticolous epiphytic growth are seen to set off the trees which were studied into two distinct groups. The first of these, characterized by a dry bark (comparatively) and a fairly acid reaction, is exemplified in Tsuga. The second group, with moist barks and a less acid reaction, is made up of all of the deciduous trees included in the investigation. These two natural groupings correspond to the two groups of moss unions, one group of which is confined to the conifer, Tsuga, and the other to the deciduous trees such as Liriodendron, Castanea, Aesculus, Fraxinus, and Fagus. All of the evidence points to bark moisture and secondarily, hydrogen-ion concentration as being the two factors most important in the distribution of corticolous bryophyte communities.

Zonation and Succession

As brought out by the maps and the discussion of the results of the bryophytic community studies, these bryophytic unions occupy certain characteristic locations on the butts of mature trees. For instance, on Liriodendron, unions of *Neckera pennata* are scattered about on the more or less bare bark of the upper part of the butt, unions of *Campylium chrysophyllum* and *Anomodon attenuatus* are grouped along the edge of the area of bare bark and a little closer to the ground, and unions of *Thuidium delicatulum* and *Hylocomium brevirostre* occur at the base of the butt very close to the soil line. The bark of any individual tree has been shown experimentally to be

several times as moist near the base of the butt as it is six feet above the soil line. The hydrogen-ion concentration in the bark of these same trees has been shown to be the same at six feet as it is closer to the ground. The result, then, is a rather definite zonation of bryophyte communities dependent on differences in bark moisture.

In the region under consideration, the driest face of the tree trunk is the west side. This has resulted in the bryophyte mat consisting of fewer zones on this side than on any of the others since only those mosses and liverworts able to survive on dry bark are present and then at lower heights than on other faces of the trunk. Correspondingly, on the eastern faces of the trunks, the more mesophytic bryophyte communities are able to extend much higher

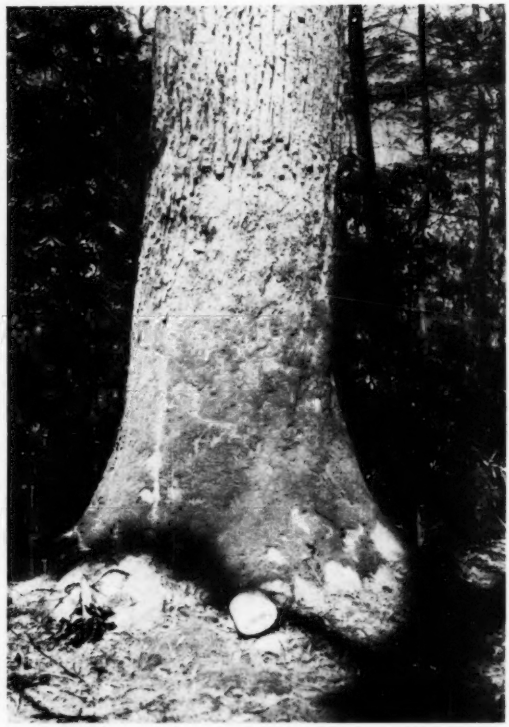

Fig. 12. Lower portion of trunk of mature *Liriodendron tulipifera*. Note sloughing-off of fissured bark, leaving a relatively smooth soft bark on the butt. A bryophytic mat covers most of this soft bark, being absent from only the more recently exposed part. This particular bryophytic mat consists mainly of *Anomodon attenuatus*. The tree measures almost seven feet in diameter breast-high.

up the base of the trunk. Thus, the directional, as well as the vertical, zonation is dependent on bark moisture. The vertical distribution of communities develops to its fullest extent only on the moist eastern faces of the trunk.

This zonation, while seemingly stable, is not static. The young Liriodendron, with its firm bark which gradually becomes fissured with age, bears only the more xerophytic bryophytes. As the tree matures, the fissured bark sloughs off of the butt leaving a softer, more sponge-like bark whose greater moisture-holding power enables the more mesophytic bryophytes to become established. Since this sloughing-off begins at the bottom and then proceeds upward to a height of six to ten feet (as illustrated by a typical mature Liriodendron in Fig. 12), the more mesophytic mosses first obtain a foothold at the base of the butt and then gradually replace the more xerophytic mosses above them as the bark becomes more suitable. Thus, a very slow succession is initiated and continues as the tree grows older, although, it is not always necessary for pioneer mosses to precede those which will form unions on medium-moist sites. Thus, sometimes *Campylium* and *Anomodon attenuatus* unions will extend out on the bare bark and surround colonies of Neckera if bark conditions reach the proper stage. The relic Neckera colonies (See map, Fig. 2) are gradually overgrown by the Campylium or the Anomodon and disappear. In this way, one bryophytic zone is slowly replaced by a more mesophytic zone and this succession is not always dependent on the changes wrought in the bark by the preceding community but to a great extent is the result of the natural ageing of the bark. It is somewhat the same, although on a smaller scale and occurring more rapidly (within the lifetime of the tree), as the very slow change in the vegetation accompanying the maturing of soils. As it approaches the five- to six-foot-level above the ground, this slow succession of bryophytic zones gradually slows down and may even halt due to the greater evaporation at this height which offsets the advantages gained by a softer bark. When this equilibrium between the bryophyte communities and the moisture factors is reached in all zones, it might be said that the bryophytic mat consists of several micro-climaxes each adapted to its own micro-climate and micro-habitat, i.e. a micro-climax swarm.

Summary and Conclusions

1. Bryophytic mats on the butts of virgin forest trees in the Greenbrier Wilderness of the Great Smoky Mountains were mapped according to unions dominated by one or two species. The trees on which these unions were mapped consisted of four examples of *Liriodendron tulipifera,* two of *Tsuga canadensis,* and one each of *Aesculus octandra, Castanea dentata, Fagus grandifolia,* and *Fraxinus americana.*

2. Bark samples were collected from heights of 3 feet, 4-5 feet, and 6 feet on both the north and south faces of each trunk. These samples were taken to the laboratory in metal cans for the determination of field moisture content. The bark samples were later used to determine the water-holding capacity, rate of drying-out, rate of absorption, and hydrogen-ion concentration of the bark.

3. Unions of *Neckera pennata, Anomodon attenuatus,* and its facies of *Anomodon rostratus* were present on every individual deciduous tree studied. The first occurred as isolated communities on the upper part of the butt and farther up the trunk. The two types of Anomodon communities were characteristic of the medium-moist sites below the Neckera patches. Unions of *Campylium chrysophyllum, Brachythecium oxycladon,* and *Fissidens cristatus,* while not found on every deciduous individual, were confined to this type of tree and not present on Tsuga. The Campylium communities were usually found on fairly dry bark while the other two types occurred near the base of the butt on definitely moist bark.

4. Communities of *Ulota crispa, Dicranum fulvum-Bazzania denudata, Hypnum reptile, Bazzania trilobata,* and *Mnium hornum* were exclusive to the bark of Tsuga. The first of these communities occurred on the upper part of the butt while the latter two were found near the base and on the tops of the larger roots. Unions of *Hylocomium brevirostre* and *Thuidium delicatulum* were present on both deciduous and conifer trees near the base of the butt.

5. The bark of Liriodendron contained the greatest amount of moisture in field condition. The bark of Tsuga was by far the driest in field condition. The barks of Liriodendron and Castanea were capable of holding the largest amounts of water while that of Tsuga held the least. Tsuga bark reached an air-dry condition in approximately one-third of the time taken by that of Liriodendron and Castanea to reach a similar state. The barks of Liriodendron and Castanea absorbed the most moisture from a saturated atmosphere and Fagus and Tsuga absorbed the least amounts. In field condition, there was a moisture gradient from very moist bark near the base of the butt to dry bark at a height of six feet. The bark at or near the base of the butt sometimes contained almost eight times as much moisture as that at a height of six feet. The eastern faces of the trunks were usually the most moist due, probably, to rain being driven against the trunks by down-drafts of cold air from the upper part of the valley.

6. The most acid of the barks was that of Tsuga ranging between pH 4.28 and pH 4.96. The barks of the deciduous trees ranged mostly between pH 5. and and pH 6. with that of Aesculus being the least acid. No gradient was obseerved in the hydrogen-ion concentration, the bark at six feet being practically the same as the bark near the base of the butt.

7. The absence of the characteristic deciduous-tree bryophyte unions from the bark of Tsuga seems to be due to the more dry and more acid bark of the latter tree. Communities of *Hylocomium brevirostre* and *Thuidium delicatulum* occurred on Tsuga only where the tree was very close to a stream.

8. The bryophyte communities form a zonation on the butts of the trees due to differences in bark moisture. These zones may slowly replace each other as the bark matures. This replacement is partly due to a betterment of bark moisture conditions due to natural ageing of the bark accompanying growth of the tree. This slow succession may come to a halt when the meso-

phytic mosses reach a height where desiccating winds counter-balance any improvement in bark moisture due to bark change. When this state of equilibrium is reached in all of the bryophyte unions on the butt, the bryophyte mat may be said to consist of a series of micro-climaxes, each adapted to its own micro-climate and micro-habitat.

ACKNOWLEDGMENT

The authors wish to express their sincere appreciation to Dr. Stanley A. Cain of the University of Tennessee for his many helpful suggestions throughout the whole course of this research. They also wish to thank Mr. A. J. Sharp of the same University who checked many of the bryophytes collected in the study of the communities, and Dr. W. C. Steere of the University of Michigan for a number of valuable suggestions. The writers are also deeply indebted to Dr. Cain and Mr. Sharp for reading the manuscript of this paper.

UNIVERSITY OF NEVADA
AND
CARLTON COLLEGE.

REFERENCES

CAIN, STANLEY A. 1938—The cove hardwood forest complex of the Great Smoky Mountains. Unpublished ms., The University of Tennessee.

——— AND W. T. PENFOUND. 1938—Aceretum rubri: The red maple swamp forest of Central Long Island. Amer. Mid. Nat. **19**:390-416.

——— AND A. J. SHARP. 1938—Bryophytic unions of certain forest types of the Great Smoky Mountains. Amer. Mid. Nat. **20**(1):249-301.

GAMS, H. 1932—Bryo-cenology. In Verdoorn, Fr., Manual of Bryology, Martinus Nijhoff, The Hague, pp. 323-366.

GLEASON, H. A. 1936—Is the synusia an association? Ecology **17**:444-451.

OLSEN, C. 1917—Studies on the succession and ecology of epiphytic bryophytes on the bark of common trees in Denmark. Bot. Tidskr. **34**:313-342. (In Danish with English summary) n. v.

RICHARDS, P. W. 1932—Ecology. In Verdoorn, Fr., Manual of Bryology. Martinus Nijhoff, The Hague, pp. 367-395.

SHARP, A. J. 1938—List of Tennessee bryophytes. Unpublished ms., The University of Tennessee.

SIRGO, V. 1935—Emajõe alamjooksul Peipsiäärsel madalikul asuvaist taimeühinguist. English summary: Plant unions of the swamps at the mouth of the river Emajõgi. Acta Instituti et Horti Botanici Universitatis Tartuensis **4**(3-4):1-64.

WILSON, B. L. 1936—A bryocoenological study of some epiphytic mosses of a Central Indiana woods. Butler Univ. Bot. Stud. **3**:149-171.

Notes on Plantago in the Pacific States

Louis C. Wheeler

PLANTAGO RHODOSPERMA Decaisne, DC. Prod. **13(1)**:722. 1852, has not been reported, as such, from California. It has been reported as *P. virginica* L. by Munz, Man. So. Calif. Bot., 489. 1935, from "San Diego, *Brandegee,* and Corona del Mar, *Davidson.*" Davidson & Moxley, Fl. So. Calif., 340. 1923, report presumably the same Davidson collection as *P. occidentalis* Decaisne, which Pilger, Pflanzenreich IV, **269**:226. 1937, gives as a synonym of *P. myosuros* Lamarck, a South American species. Although Decaisne, idem, stated that *P. occidentalis* came from North America, Pilger, idem, expresses the opinion that there must have been an error as to the source of the type. In any event the Californian plant is not *P. occidentalis* for that was described as having three fuscous seeds in each capsule while *P. rhodosperma* has two reddish seeds in each capsule.

The following collections of *P. rhodosperma* from the Pacific States are in Gray Herbarium: California, San Diego Co.: San Diego, May, 1882, *C. R. Orcutt 128,* May 20, 1903, *T. S. Brandegee* (Pl. Pacific Coast Dist. by C. F. Baker, No. 3409); Sweetwater Valley, May, 1884, *D. Cleveland.* Co.? Piñasquitos, *Geo. Thurber 583* in 1852.

PLANTAGO VIRGINICA L. is represented in Gray Herbarium by the following collections from the Pacific States: California, Shasta Co.: Near Redding, May 30, 1905, *A. A. Heller 7896.* Oregon: Curry Co.: Dry bank along Chetco River three miles above Harbor, July 12, 1919, *M. E. Peck 8803;* Dry soil, two miles south of Illahe, along trail, June 21, 1917, *J. C. Nelson 1362;* Open ground near river, Agness, June 22, 1917, *J. C. Nelson 1447.*

The following key will serve to separate *P. rhodosperma* from its relatives (members of Plantago sect. Novorbis) in the Pacific States:

Plant annual; capsules 2-seeded; face of seed plane or concave.
Seeds reddish (Brazil red,[1] garnet brown, Morocco red, to claret brown), 2.5-2.75 mm. long ---------- *P. rhodosperma*

Seeds brownish (cinnamon-rufous, tawny, ochraceous tawny), 1.5-1.75 mm. long ---------- *P. virginica*

Plant perennial; capsules 3-seeded; face of seed convex. *P. Durvillei* Del. ex F. & M. ssp. *subnuda* (Pilger) Pilger (= *P. hirtella* HBK sensu Calif. authors in large part fide Pilger). Type locality: Pacific Grove in pine woods, Monterey Co., California. . . . var. *angustata* Pilger. Type loc.: San Francisco. *P. hirtella* HBK var. *Galeottiana* (Dcne.) Pilger. Type loc.: Mexico.

---

1 Ridgway, Color Standards and Nomenclature, 1912.

The differentiae given by Pilger to separate *P. Durvillei* from *P. hirtella* are a trifle subtle. The characters used to distinguish the group in which *P. Durvillei* is placed from that in which *P. hirtella* is placed are respectively:

I. Radix primaria fusiformis perpetue conservata; fere semper indivisae, plantae parvae.

III. Caudex brevis; radix primaria in specim. adultis O vel si diutius conservata, radicellis long superata.

Yet Pilger characterizes *P. Durvillei* ssp. *subnuda* which comes under I: "Radix in specim. mihi visis haud evoluta." It is consequently difficult to separate the two in the key, and collections from California cited by him as representing both species are apparently identical.

Pilger's treatment of what Poe, Bull. Torr. Bot. Club **55**:406. 1928, called the "Plantago Patagonica group of the United States and Canada" is of particular interest in this area. The main difference between the two treatments is Pilger's recognition of more species. Probably this was made possible by examination of fewer specimens combined with the exercise of a narrower viewpoint as to what constitutes a species. In Pilger's key, l.c., 339, separating some of these species, six parallel choices are used. This saved space but certainly adds to the difficulty of separating these doubtful species.

Pilger made an error in his nomenclature for, l.c., 373, he rejected *Plantago insularis* Eastwood, Proc. Calif. Acad. Sci. III 1:112. 1898, because he thought it was preoccupied by *P. insularis* (Godr.) Nyman, Conspectus Fl. Eur., 618. 1881.[2] The name was based on *P. subulata* L. *β insularis* Godron in Grenier & Godron, Fl. France, 725. 1850. This varietal name was abortive since in synonymy was cited *P. incana β capitellata* Salzmann, Beiblätter zur Flora oder Bot. Zeit. 1834, **2**:12. 1834. However, a name can be validated by a change in rank though it is doubtful whether an abortive name can ever be validated. But the error here was in the interpretation of Nyman's combination. Under his "13. P. subulata L." appears in smaller type: "*P. insularis (G. G.)." The thing that has been overlooked is that in the front of the book Nyman explains his symbols and the explanation applicable here is: "Subspecies ideo (litteris minimis impressae) notantur asterisco (*)," Hence Nyman really made the combination *P. subulata* L. subsp. *P. insularis* (Godr.) Nyman. That this combination was invalidated because it was a subdivision of a species proposed as a binomial is of no concern here.[3] The first use that Pilger, l.c., 207, and in *litt., v. i.*, gives of the *"P. insularis"* after Nyman is that of Briquet, Ann. Conserv. & Jardin Bot. Genev. **5**:112. 1901. Briquet attributed the name in specific rank to Nyman presumably because he was laboring under the same misapprehension as Pilger. Briquet's use presumably validated in specific rank *P. insularis* (Godr.) if an originally

---

2 Date given on signature cover to part III in the copy at Gray Herbarium. Stearn, Jour. Bot. Brit. **76**:113. 1938, adds the information that it was probably published in July.

3 International Rules of Botanical Nomenclature, Art. 28.

abortive name can be validated. But *P. insularis* Eastwood, 1898, is earlier and is valid for our plant. A query addressed to Pilger secured a statement, dated March 1, 1938, of his position. He maintains that a binomial preoccupies a binomial regardless of rank. According to the Rules only names of the same rank are considered for purposes of priority. Pilger raises the issue of collective species with their included minor species which have been used by some of the botanists of Central Europe. I leave them to find their way out of the system they have created. The International Rules of Botanical Nomenclature do not recognize their system in which *Gesamtarten* are substituted for series or subseries. But Nyman was not using collective species. He merely used binomials as subspecies, varieties, and subvarieties, as well as for species. Since, for purposes of priority, only names of the same rank are considered, a subspecific name cannot preoccupy a specific name. It is true that binomials should be used only as specific names but the use of a binomial to designate a subdivision of a species does not make the name of specific rank but rather makes the name invalid in the rank proposed.

The writer is indebted to Professor M. L. Fernald for valuable bibliographic suggestions.

GRAY HERBARIUM,
HARVARD UNIVERSITY,
CAMBRIDGE, MASSACHUSETTS.

Creosote Bush and the Lower Sonoran Zone of the Southwest

Joseph Ewan

Creosote Bush (*Larrea divaricata* Cav.)[1] is among the most reliable of "indicators" of natural biologic areas in the Southwest, delimiting the Lower Sonoran Zone fairly sharply. The recent articles[2] on the effect of sustained subzero weather upon *Larrea* in the Virgin River Valley of Utah suggest certain earlier studies made upon this shrub. For more than half a century this remarkable Sonoran species has commanded ecological, distributional, chemical, as well as systematic, studies from a score of workers. Among the earliest of these investigations was that published by J. M. Stillman in 1880[3] upon the chemical nature of the gum secreted by the *Larrea* stems. Recent digests of the systematic and broad ecologic status of the shrub have been drawn up by Shreve in 1931[4] and by Jepson in 1936.[5] Volney M. Spalding treated the relation of the Creosote Bush to water supply with particular reference to Arizona.[6] Shreve and Mallery have reported on work in progress upon the controlling factors limiting the distribution of the shrub.[7] They report "substantial differences in environment exist within the space occupied by a single individual." Accordingly, it is difficult to assign the determining agency limiting distribution, even over a small portion of its range in the Southwest. Osmotic values for the leaves have been determined by Mallery[8] and their relation to soluble salts in the soils, mechanical and chemical nature of the soil and influence of rainfall and soil moisture, both through the day and seasonally. Material for these osmotic studies was collected over practically the entire range of the Creosote Bush in the Southwest. As has been pointed out several times the occurrence of *Larrea* over thousands of square miles of arid or desert country, where it is often a dominant species showing considerable "physiological elasticity" in its habitat requirements, is proof that it is one of the most successful of desert perennials.

The fact has been pointed out by Shreve[9] that this small-leaved non-succulent evergreen lacks the anatomical characters common to desert plants in general that favor the conservation of water. Shreve says "the adjustments

1 Johnston (Proc. Calif. Acad. Sci. ser. 4, 12:1053. 1924) has pointed out that the South American plant, the first named, is not distinguishable from our shrub.

2 W. P. Cottam, *Science*, 86:563-564, June 11, 1937; F. R. Fosberg, *ibid.* 87:39-40, Jan. 14, 1938 and A. M. Woodbury, *ibid.* 87:484-485, May 27, 1938.

3 Am. Chem. Jour. 2:34-38. 1880.

4 *Die Pflanzenareale*, Reihe 3. Heft 1, Karte 5. 1931.

5 *A Flora of California* 2:437-438. 1936.

6 Bot. Gaz. 38:122-138. 1904.

7 Annual Rept. Div. Pl. Biol., Carn. Inst. Wash., 1934-35, p. 210. 1935.

8 Ecological Monographs 5:1-35. 1935.

9 Scientific Monthly 42:203. 1936.

of *Larrea* to its arid environment are chiefly functional rather than structural." Surely this lack of anatomical reservoirs in its leaves stands the shrub in good stead during prolonged subzero temperatures. Relatively low water content in the leaves favors frost resistance. Death from freezing in plants primarily follows the formation of ice crystals in the intercellular spaces followed by a desiccation of the cells. Death by freezing, then, is analogous with death from drought. This and cognate matters of frost resistance, "free water" and "bound water," are tersely discussed by Maximov.[10] As for drought resistance *Larrea* is again victor. Of several accounts on the effects of protracted drought on the species Jaeger's account[11] will suffice. He describes a drought in the Bagdad region of Mohave Desert of thirty two month's duration (1909-1912) without registerable precipitation. The drought exerted a withering but not lethal effect on the *Larrea* population.

Robert F. Griggs published a study[12] of the "behavior of some species at the edges of their ranges" in Fairfield and Hocking counties, Ohio, and identified what he termed "tension zones" between different species. In these zones along the limits of their ranges species may be observed advancing while others are "being beaten back" and he suggests that a study of these marginal areas will determine the trend of geographical movements. It will be seen by an examination of Shreve's map (*Die Pflanzenareale,* Reihe 3, Heft 1, Karte 5) that *Larrea divaricata* is on the margin of its range in the Virgin River Valley. The writer is familiar with the shrub in another marginal area, the western borders of the Mohave Desert of California. Here it favors the piedmont mesas and broad bajadas issuing upon the desert from the coastal mountains. Its tension zone here is characterized by a strong intrusion of populations of Rabbit Brush (*Chrysothamnus nauseosus* subsp.) and of Saltbush (*Atriplex canescens*). In certain areas to the eastward, that is, on the gentle slopes of the old Pleistocene lake basins of the central Mohave Desert, *Larrea* forms pure stands of monotonous ubiquity. A close study of *Larrea* along such tension zones will yield facts of significance toward understanding the factors limiting its distribution and its persistence in the areas it now occupies. Photographic records taken of individuals, such as kept over a thirty year period by Shreve and Hinckley,[13] will furnish evidence on life span. Longevity figures may reasonably be expected to vary over the wide range of the species even in North America. In the vicinity of the Desert Laboratory, Tucson, Arizona, it was found that "the largest [Larreas] have undergone little change in size and bulk [in thirty years]. . . . It seems safe to infer that large individuals are generally well in excess of 100 years of age." Apparently the Creosote Bush is an oldtime resident in its present range and remarkably stable, physiologically, as a species. Its great morphologic uniformity over its wide range in two hemispheres is testimony of its organic stability.

10 *The Plant in relation to Water*, 244 *et seq.* 1929.
11 *California Deserts*, 133, 1933.
12 Bull. Torr. Club 41:25-49. 1914.
13 Ecology 18:474-475. 1937.

UNIVERSITY OF COLORADO.

Some Blood Parasites from Birds of the Lake Okaboji Region*

G. Robert Coatney

The material for the present paper was collected during the summers of 1935 and 1936, while the author was a guest investigator at the Iowa Lakeside Laboratory. The author takes this opportunity to thank the Associate Director, Dr. L. O. Nolf, for his kindness in providing laboratory space for these studies.

Altogether, sixty-three different birds were examined, representing fifteen families and twenty-three species. Among these, seven were positive for one or more genera of blood protozoa.

The methods used in collecting and studying the material, and the determination of the vernacular and scientific names of the hosts are the same as outlined by Coatney and Roudabush (1937).

Haemoproteus

Halteridium parasites were found in four species of birds. *Haemoproteus noctuae* var. *cellii* was found in a Screech Owl *(Otus asio)*, *H. noctuae* var. *nebraskensis* in one Great Horned Owl *(Bubo virginianus)*, out of three examined, *H. velans* in a Northern Flicker *(Colaptes auratus luteus)* and *H. beckeri* in a Brown Thrasher *(Toxostoma rufum)*.

The infection in the screech owl was etremely heavy, with 12 to 14 parasitized cells per oil field. Many of the erythrocytes carried multiple infections with parasites of approximately the same size, although those carrying both mature and young gametocytes were not uncommon. The bird seemed unaffected by the large number of parasites and was released after being under observation for about a day.

Leucocytozoon

Leucocytozoon iowense sp. nov.

Pl. 1. Figs. 1-2.

Leucocytozoon parasites in circular host cells were found in one Eastern Green Heron *(Butorides virescens)*. The cytoplasm of the female gametocytes stained a dark blue and the nuclei a reddish pink. The karyosome stained a deep red. The nucleus was generally oval in outline with a karyo-

* A contribution from the Iowa Lakeside Laboratory and the Department of Biology, State Teachers' College, Peru, Nebraska.

some lying almost outside the nucleus. The parasites measured 10.90μ to 16.67μ in length and 8.33μ to 13.14μ in width. The average was 13.40μ by 11.03μ. The nucleus varied from 3.21μ to 6.41μ in length and from 1.60μ to 3.85μ in width with an average of 2.82μ by 4.24μ. The karyosome had an average measurement of 1.09μ by 1.50μ.

The microgametocytes stained a light blue and their nuclei pink. The nucleus was round to oval. These parasites varied in length from 10.26μ to 14.42μ, and in width from 10.26μ to 12.82μ. The average measurement was 11.29μ by 12.68μ. The length range of the nucleus was 4.17μ to 6.41μ and the width, 2.24μ to 4.49μ. The average was 3.42μ by 4.92μ.

Leucocytozoon parasites have been reported from at least five genera of herons (see Coatney, 1937), although only one other species has been named. Rodhain, Pons, Vandenbranden and Bequaert (1913) described *L. ardeae* from *Ardea goliath*. The female parasites of this form were described as having a large, elongate nucleus with a distinct karyosome. The measurement given for the female parasites was 14μ by 17μ. The microgametocytes measured 16μ by 17μ and had a star shaped nucleus.

L. iowensis differs from *L. ardeae* in being significantly smaller in all dimensions plus the fact that the macrogametocytes had an oval nucleus in contrast to an elongate nucleus in *L. ardeae*, and the microgametocytes had a round to oval nucleus in contrast to star-shaped in the males of *L. ardeae*.

Leucocytozoon sp.

Pl. 1. Figs. 3-4.

Two immature Black-crowned Night Herons *(Nycticorax nycticorax hoactli)* were examined during the course of this survey and both were found harboring Leucocytozoa in circular host cells. The macrogametocytes stained blue and were without vacuoles. The circular nucleus stained pink. A round to oval karyosome was present and located decidedly off center and, in many examples, barely in contact with the nucleus. These parasites had a measurement range of 11.54μ to 18.59μ in length and from 5.77μ to 13.46μ in width, with an average of 11.09μ by 14.04μ. The range for the nucleus was 3.53μ to 7.05μ in length and from 2.56μ to 4.81μ in width. The average for the nucleus was 3.35μ by 5.27μ. The mean for the karyosome was 0.91μ by 1.24μ.

The microgametocytes stained pink. The nucleus was decidedly diffuse and stained with almost the same intensity as the cytoplasm so that in some cases the boundary could not be made out with certainty. The parasites varied in length from 12.81μ to 18.59μ and in width from 7.69μ to 12.18μ. The mean was 9.74μ by 14.77μ. The range for the nucleus was 5.77μ to 9.62μ in length and the width from 3.21μ to 5.77μ with a mean of 4.41μ by 7.57μ.

Aubert and Heckenroth (1911) first reported Leucocytozoa in the Black-crowned Night Heron from French Equitorial Africa. The parasites were

located in circular host cells and the macrogametocytes had a mean size of 11μ-22μ. No karyosome was present. The microgametocytes had a mean size of 16μ-20μ. Franchini (1924) reported these parasites in the same bird from Italy. This author did not record the measurements of these parasites, but indicated that they compared favorably with his measurements of the Leucocytozoon parasites from *Ardea purpurea*. Franchini's figures show a karyosome in the macrogametocytes.

Plasmodium sp.

Pl. 1. Figs. 5-12.

One Forster's Tern *(Sterna forsteri)*, out of four examined, carried a light plasmodial infection. The young trophozoites were found near the poles of the erythrocytes. The schizonts were rounded to elongate and generally occupied a polar position. The segmenters had four to six merozoites, four being the most common. The host cell nucleus was not disturbed.

The elongate macrogametocytes were generally serrated in outline and showed a tendency to curve around the host cell nucleus. The granules were spheroidal. The cytoplasm stained dark blue with Giemsa. The microgametocytes were generally not serrate; the granules spheroidal. The cytoplasm remained almost colorless with Giemsa.

This is believed to be the first record of a plasmodium from any member of the sub order Lari, which includes the skiras, gulls, and terns.

Trypanosoma

Trypanosoma avium

Trypanosomes were encountered in the Black-crowned Night Heron *(Nycticorax nycticorax hoactli)*, the Eastern Green Heron *(Butorides virescens)*, and the Screech owl *(Otus asio)*. The specimens from the herons were all non-myonemed, and those from the owl were myonemed. All the tryponosomes are considered to be *T. avium*. The measurements of all specimens are given in Table 1.

The following birds were negative for blood protozoa: (3 im.) Eastern Red-tailed Hawk *(Buteo borealis borealis)*; (9 im.) Marsh Hawk *(Circus hudsonius)*; (2) Great Horned Owl *(Bubo virginianus virginianus)*; (2 im.) Western Burrowing Owl *(Speotyto cunicularia hypugaea)*; (1) European Partridge *(Perdix perdix perdix)*; (3 im., 14 ad.) Yellow-headed Blackbird *(Xanthocephalus xanthocephalus)**; (1) Bronzed Grackle *(Quiscalus quiscula aeneus)*; (1) Red-headed Woodpecker *(Melanerpes erythrocephalus)*; (1) Arkansas Kingbird *(Tyranus verticalis)*; (4) Bank Swallow *(Riparia riparia riparia)*; (3) Forster's Tern *(Sterna forsteri)*; (2) Black Tern *(Chlidonias nigra surinamensis)*; (1) Ring-billed Gull *(Larus delawarensis)*; (1 im., 1 ad.) Eastern Robin *(Turdus migratorius migratorius)*; (1) Western Solitary

* I am indebted to Dr. G. A. Ammann, of the University of Michigan, for smears from these seventeen birds.

Sandpiper *(Tringa solitaria cinnamonea)*; (1) Northern Blue Jay *(Cyanocitta cristata cristata)*; (1) Little Blue Heron *(Florida caerula caerula)*; (1) Red-breasted Grosbeak *(Hedymeles ludovicianus)*; (1) Catbird *(Dumatella carolinensis)*.

REFERENCES

AUBERT, P. AND F. HECKENROTH. 1911—Sur trois *Leucocytozoon* des oiseaux du Congo Francais. C. R. Soc. Biol. **70**:958-959.

COATNEY, G. ROBERT. 1937—A catalog and host-index of the genus Leucocytozoon. Jour. Parasit. **23**:202-212.

COATNEY, G. ROBERT AND ROBERT L. ROUDABUSH. 1937—Some blood parasites from Nebraska birds. Am. Midl. Nat. **18**:1005-1030.

FRANCHINI, G. 1924—Observations sur les Hématozoaires des oiseaux d'Italie. Ann. Inst. Pasteur. **38**:470-515.

RODHAIN, J., C. PONS, F. VANDENBRANDEN, J. BEQUAERT. 1913—Notes sur quelques hématozoaires du Congo Belge. Arch. Protist. **29**:259-278.

TABLE 1

Trypanosoma avium

Measurements of Specimens from Various Hosts.

		Without Myonemes		With Myonemes
		Black-crowned Night Heron (6)	Green Heron (7)	Screech Owl (3)
Posterior end to middle of parabasal body	Range	1.32μ–2.97μ	1.32μ–6.60μ	7.59μ–11.88μ
	Aver.	2.53μ	5.09μ	9.68μ
Middle of parabasal body to middle of nucleus	Range	5.28μ–8.91μ	5.94μ–10.56μ	9.90μ–14.19μ
	Aver.	7.91μ	8.01μ	12.85μ
Middle of nucleus to anterior end of body	Range	9.24μ–12.21μ	9.24μ–15.18μ	25.74μ–29.70μ
	Aver.	10.24μ	11.83μ	27.28μ
Length of flagellum	Range	5.28μ–6.60μ	5.94μ–8.58μ	3.30μ–4.29μ
	Aver.	5.64μ	7.59μ	3.96μ
Length (sum of the separate measurements)	Aver.	26.32μ	32.52μ	53.77μ
Width	Range	5.28μ–10.23μ	3.96μ–7.59μ	4.95μ–5.94μ
	Aver.	6.93μ	7.41μ	5.28μ
Length of the nucleus	Range	4.29μ–5.94μ	3.63μ–6.93μ	3.63μ–3.96μ
	Aver.	4.78μ	5.00μ	3.74μ
Width of the nucleus	Range	3.30μ–3.63μ	1.98μ–4.62μ	3.30μ–3.63μ
	Aver.	3.52μ	3.16μ	3.41μ

The figure in brackets denotes the number of specimens found and measured.

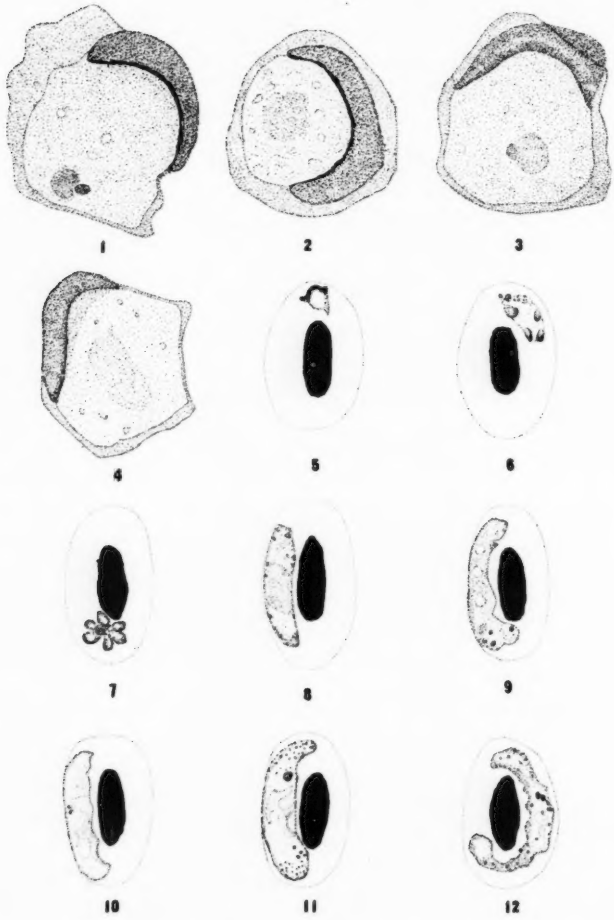

PLATE 1. (Camera lucida drawings, all figures x 1750).

Figs. (1-2) *Leucocytozoon iowensis* from the Eastern Green Heron. A macro- and microgametocyte. Figs. (3-4) *Leucocytozoon* sp. from the Black-crowned Night Heron. A macro- and microgametocyte. Figs. (5-12) *Plasmodium* sp. from Forster's Tern. Fig. 5 trophozoite, Figs. 6-7 schizonts, Figs. 8-10 immature gametocytes, Fig. 11-12 mature gametocytes.

The North American Fresh-Water Tetraonchinae*

John D. Mizelle and R. Chester Hughes

Introduction

Definite taxonomic investigation of the North American fresh-water Tetraonchinae began with the description of *Urocleidus aculeatus* (Van Cleave and Mueller, 1932). At the present time 9 genera, namely, *Cleidodiscus, Urocleidus, Onchocleidus, Leptocleidus, Tetracleidus, Aristocleidus, Haplocleidus, Pterocleidus,* and *Actinocleidus* (all of Mueller) and 49 species belonging thereto, have been described by Mueller (1934, etc.), Mizelle (1936, etc.) and Summers (1937). In addition one new species in each of two other genera, *Tetraonchus* Diesing and *Murraytrema* Price, already known in Europe and Australia respectively, has been found in this country. Besides these 11 groups the subfamily also contains 6 marine and 4 foreign fresh-water genera. The latter are the European *Dactylodiscus* Olsson, 1873, and the Australian *Daitreosoma, Empleurosoma,* and *Anchylodiscus* of Johnston and Tiegs (1922). The marine and foreign genera, adequately reviewed by Price (1937b), are not discussed in this paper.

The study of fresh-water Tetraonchinae in this country is quite young but much progress has recently been made. Since the descriptions of the above-mentioned genera and species occur in scattered publications, it is deemed appropriate to summarize the field, correct outstanding taxonomic inconsistencies, and prepare usable keys to the North American forms. The validity of some of the putative American genera has already been questioned (Price, 1937b; Mizelle, 1938a,b). We are of the opinion that the 9 above-listed Muellerian genera really embrace only 3 natural groups of generic magnitude for which the names *Cleidodiscus, Urocleidus,* and *Actinocleidus* should be retained.

We have based our proposed revision on two arbitrary assumptions, first, that more than one structural difference is necessary to justify the establishment of a new genus, and second, that sexual characters have more taxonomic value than the sporadic occurrence of spines or spurs on, or differences in size or shape of, certain haptoral parts.

We use the terms *anchor, hook, bar,* and *accessory piece* as used by Mueller (1936a); *copulatory complex* as by Mizelle (1936); and *haptor* as by Price (1934).

The genus *Tetracleidus* was "distinguished from *Urocleidus* in the presence of a vagina; from *Cleidodiscus* in having the vagina on the right; from

* Contribution from the Zoological Laboratory, Oklahoma Agricultural and Mechanical College.

Onchocleidus in having an accessory piece in the cirrus complex" (Mueller, 1936a). Taxonomic discrepancy in these genera is seen in the following facts: in 3 of the 6 originally described species of *Onchocleidus (O. similis, O mimus,* and *O. dispar)* and in (Mueller, 1938) *Cleidodiscus malleus* no vagina was observed; the vagina in *Cleidodiscus brachus* was (Mueller, 1938) "not certainly observed. . . . but apparently on left"; a vagina was not mentioned in the description (Mueller, 1937) of *Cleidodiscus mirabilis;* the vagina is lacking in (Mueller, 1936b) *Cleidodiscus pricei* and (Mizelle, 1936) *Onchocleidus interruptus;* and in (Mueller, 1936a) *O. dispar* and in all of the several recently described (Mizelle, 1936, 1938a; Mueller, 1937) species of *Onchocleidus* the accessory piece is present. Indeed none of the features used to distinguish *Tetracleidus, Urocleidus,* and *Onchocleidus* is constantly possessed by all of the species assigned to the respective genera. We believe that the absence of a vagina in North American fresh-water forms is not of generic significance since this condition sporadically occurs in several of the old genera. Furthermore, it seems not unlikely that, with more careful study, the accessory piece will be found to occur in nearly all species of *Onchocleidus.*

The genus *Leptocleidus* was distinguished (Mueller, 1936a) by the presence of a "rounded forebody, and long tapering hindbody. . . . Haptor poorly set off from body. . . . Supporting bars rudimentary. . . . Cirrus. . . . lying in a large coil." Old specimens of *Cleidodiscus robustus* have been observed to have a rounded forebody and a relatively long tapering hindbody. Degree of separation of haptor and body has been previously considered a poor taxonomic feature (Mizelle, 1938b). The cirrus's having the form of a large coil is thought to be not of generic importance since in certain species of the old genus *Onchocleidus,* for example, *O. principalis, O. acuminatus,* and *O. helicis,* the cirrus is corkscrew-like (in reality a small coil), while in others, *O. mimus, O. distinctus,* and *O. mucronatus,* etc., the cirrus is straight. For these reasons and the further fact that the accessory piece is basally articulate with the cirrus, we are transferring *Leptocleidus megalonchus* to the genus *Cleidodiscus.*

The genus *Aristocleidus* was proposed to include a species essentially like those in *Onchocleidus* except for a larger size and different shape of the dorsal anchors as compared with the ventrals. Should differences in shape of anchors be of generic importance a new genus should be erected to include *Actinocleidus longus* in which the roots of the anterior anchors are bifurcate and those of the posterior ones are not.

Haplocleidus was split off from *Onchocleidus* to include species in which the dorsal anchors are markedly larger than the ventrals. This character would seem to be of little value since specimens of *Cleidodiscus pricei* have been found by Seamster (1938) to have this trait. Moreover, if this feature be generic importance, *Cleidodiscus brachus,* in which (Mueller, 1938, Pl. 2, Figs. 1 and 2) the ventral anchors are much larger than the dorsals, should be placed in a new genus.

The genus *Pterocleidus* was set up for *Onchocleidus*-like forms having a spur-like process on each anchor shaft. This character seems to be no more

important than spines on the bars as in *Cleidodiscus vancleavei, Cleidodiscus robustus, Onchocleidus cyanellus,* and *Onchocleidus mucronatus,* or a knob on the accessory piece as in *Cleidodiscus robustus, Cleidodiscus capax, Actinocleidus gracilis, Actinocleidus articularis,* and *Actinocleidus fergusoni.* Such characters can hardly be of generic value especially when considered separately.

It is perhaps worthy of mention that the species of *Actinocleidus* are more consistent in the possession of common characteristics than is either *Cleidodiscus* or *Urocleidus* as these genera are defined below.

The writers are grateful to Dr. Justus F. Mueller of the New York State College of Forestry and to Dr. Emmett W. Price of the United States Bureau of Animal Industry for generous loans of type material.

Systematic Account of the Tetraonchinae

The subfamily *Tetraonchinae* Monticelli, 1903, belongs to the family *Dactylogyridae* Bychowsky, 1933, superfamily *Gyrodactyloidea* Johnston and Tiegs, 1922, suborder *Monopisthocotylea* Odhner, 1912, and order *Monogenea* Carus, 1863. Price (1937b) gave the subfamily *Tetraonchinae* the following diagnosis:

> Body devoid of scales or spines. Haptor without squamodiscs, with 2 pairs of large hooks and (?) 2 to 16 marginal hooklets. Intestine single or double. Eyes present or absent. Testis usually without lobes. Ovary without lobes. Vagina present or absent.

In listing host species no attempt was made to determine the proper scientific names of fish. The host names have been copied, without change, from published reports except that (1) where the same fish has been referred to under different names we have used only one, and (2) the authorship of all specific names has been indicated. Host records have been taken from literature and recent observations.

Key to the Genera of North American Fresh-Water Tetraonchinae Monticelli, 1903

1. Gut rhabdocoele, small haptoral hooks 16, haptoral bar 1 ---------- *Tetraonchus* Diesing, 1858
   Gut bifurcate, hooks 14, bars 2 or 3 ---------- 2
2. Rami of gut not confluent posteriorly, haptoral bars 3 ---*Muarraytrema* Price, 1937
   Rami of gut confluent posteriorly, bars 2 ---------- 3
3. Haptoral bars articulate ---------- *Actinocleidus* Mueller, 1937
   Bars nonarticulate ---------- 4
4. Vagina (absent in *C. pricei* and perhaps in *C. mirabilis, C. brachus,* and *C. megalonchus*) opening on left body margin, cirrus and accessory piece basally articulate (except perhaps in *C. alatus*) ---------- *Cleidodiscus* Mueller, 1934
   Vagina (if present) opening to right, cirrus and accessory piece (if any) never basally articulate ---------- *Urocleidus* Mueller, 1934

Genus *Tetraonchus* Diesing, 1858

Synonym.—Monocoelium Wegener, 1910.

Diagnosis (quoted from Price, 1937b).—"Cephalic glands opening to exterior through several pairs of head organs. Haptor more or less distinctly

set off from body proper, with 2 pairs of large hooks supported by a single large transverse cuticular bar; 16 marginal hooklets. Intestine single, without diverticula. Eyes present. Testes and ovary in equatorial zone. Vagina absent."

Type species.—*Tetraonchus monenteron* (Wagener, 1857) Diesing, 1858.

KEY TO THE SPECIES OF TETRAONCHUS

Haptor as wide as body, haptoral bar large and butterfly-shaped, accessory piece not bifid but spirally curved distally. ---------- *T. monenteron*

Haptor half as wide as body, haptoral bar small and not butterfly-shaped, accessory piece bifid. ---------- *T. alaskensis*

Species of *Tetraonchus*

1. *Tetraonchus monenteron* (Wagener, 1857) Diesing, 1858. Synonyms —*Dactylogyrus monenteron* Wagener, 1857; *Gyrodactylus cochlea* Wedl, 1857; and *Monocoelium monenteron* (Wagener, 1857) Wegener, 1910. This species, described originally form *Esox lucius* Linnaeus in Europe, has been found on the same host in this country by Van Cleave and Mueller (1934).

2. *Tetraonchus alaskensis* Price, 1937. Reported by Price (1937a) from *Salmo mykiss* Walbaum, *Salvelinus malma spectabilis* (Girard), and *Oncorhynchus kisutch* Walbaum.

Genus *Cleidodiscus* Mueller, 1934

Synonym.—*Leptocleidus* Mueller, 1936, in part.

Diagnosis.—Tetraonchinae. Body, exclusive of haptor, somewhat flattened dorsoventrally and usually narrowly elliptical (except in *C. megalonchus* and unusual specimens of *C. robustus*) in dorsal view. Eyes 4, one pair larger than, and posterior to, the other. Gut bifurcate, without diverticula, rami confluent posteriorly. Gonads near middle of body. Cirrus usually a relatively simple chitinous tube. Accessory piece *always present* and generally *articulated basally* with the cirrus. Vagina (lacking in *C. pricei* and perhaps in *C. mirabilis, C. brachus,* and *C. megalonchus*) opening on *left margin* near middle of body. Vitellaria consisting of very numerous and very small discrete follicles arranged in a pair of lateral bands extending from pharyngeal region to, or into, peduncle; the bands always posteriorly, and sometimes anteriorly, confluent. Haptor, generally distinct (except in *C. megalonchus*), discoidal or subhexagonal; armed with 4 anchors and 14 hooks. Anchors, one pair dorsal and the other ventral, with superficial roots of each pair connected by a transverse bar; bars nonarticulate. Parasitic on gills of fresh-water fish.

Type species.—*Cleidodiscus robustus* Mueller, 1934.

The genus *Leptocleidus* was described by Mueller (1936a) for a single species, namely, *Leptocleidus megalonchus,* and distinguished from species of *Cleidodiscus* in having (1) a pyriform body, (2) the "haptor poorly set off from body," (3) the "bars rudimentary," and (4) the cirrus greatly elongate and extensively coiled. We feel that these features are relative in nature and not of generic importance. The fact that the accessory piece is basally articu-

late with the cirrus (Mueller, 1936a: Fig. 25) is further evidence that this species belongs to *Cleidodiscus*. It is regrettable that we have no information relative to the vagina in this form.

Thus far *Cleidodiscus* is known only from North America.

In *Cleidodscus malleus* Mueller, 1938, no vagina was seen, and judging from the figure (Mueller, 1938: Pl. 3, Fig. 3), a cirral thread occurs and the cirrus and accessory piece are basally nonarticulate. For these reasons we are transferring this species to the genus *Urocleidus* Mueller, 1934.

KEY TO THE NORTH AMERICAN SPECIES OF CLEIDODISCUS *

1. Cirrus elongate ---------- 2
   Cirrus short ---------- 5
2. Cirrus coiled ---------- *C. megalonchus*
   Cirrus not coiled ---------- 3
3. Accessory piece sleeve-like, partially enclosing cirrus ---------- 4
   Accessory piece not sleeve-like ---------- *C. namatocirrus*
4. Bases of dorsal and ventral anchors of approximately equal width--*C. uniformis*
   Bases o fventral anchors distinctly wider than dorsals ---------- *C. longus*
5. Accessory piece chelate ---------- *C. bedardi*
   Accessory piece nonchelate ---------- 6
6. Cirrus with a single digitiform projection at base, accessory piece distally tridigitate ---------- 7
   Cirrus without a basal projection, accessory piece not tridigitate ---------- 8
7. Middle digit of accessory piece with a single hook ---------- *C. floridanus*
   Middle digit of accessory piece bearing two hooks ---------- *C. mirabilis*
8. Accessory piece with a conspicuous knob ---------- 9
   Accessory piece without knob ---------- 11
9. Cirrus sickle-shaped ---------- *C. diversus*
   Cirrus not sickle-shaped ---------- 10
10. Cirrus and accessory piece entwined ---------- *C. capax*
    Cirrus aand accessory piece not entwined ---------- *C. robustus*
11. Cirrus sickle-shaped ---------- 12
    Cirrus not sickle-shaped ---------- 13
12. Dorsal bar slightly larger than ventral, vagina absent ---------- *C. pricei*
    Ventral bar much larger than dorsal, vagina present ---------- *C. alatus*
13. Cirrus trumpet-shaped ---------- *C. stentor*
    Cirrus not trumpet-shaped ---------- 14
14. Bars with prominent median posterior spines ---------- *C. vancleavei*
    Bars not spined ---------- *C. brachus*

North American Species of *Cleidodiscus**

1. *Cleidodiscus robustus* Mueller, 1934. Synonym—*Cleidodiscus incisor* Mizelle, 1936 (see Mizelle, 1938b). Hosts—*Eupomotis gibbosus* (Linnaeus), *Helioperca macrochira* (Rafinesque), *Apomotis cyanellus* (Rafinesque), and "bass."

* Since this manuscript was completed, descriptions (Price, 1938) of two new species in this genus, *Cleidodiscus travassosi* and *Cleidodiscus chavarriai*, from Latin America have appeared. These forms are not included in this paper.

2. *Cleidodiscus megalonchus* (Mueller, 1936) nobis. Synonym—*Leptocleidus megalonchus* Mueller, 1936. Host—*Micropterus dolomieu* Lacépède. Belonging perhaps to this species were specimens from the same host reported by Cooper (1915) as "*Ancyrocephalus paradoxus* Creplin," and from *Ambloplites rupestris* (Rafinesque) and *Eupomotis gibbosus* (Linnaeus) by Stafford (1905) as "*Tetraonchus unguiculatus* Wag."

3. *Cleidodiscus capax* Mizelle, 1936, from *Pomoxis sparoides* (Lacépède) and *Pomoxis annularis* Rafinesque.

4. *Cleidodiscus longus* Mizelle, 1936, from *Pomoxis annularis* Rafinesque.

5. *Cleidodiscus uniformis* Mizelle, 1936, from *Pomoxis annularis* Rafinesque.

6. *Cleidodiscus vancleavei* Mizelle, 1936. Synonym—*Onchocleidus formosus* Mueller, 1936, and *Cleidodiscus formosus* (Mueller, 1936) Price, 1937—see Mizelle (1938b). Hosts—*Pomoxis annularis* Rafinesque and *Pomoxis sparoides* (Lacépède).

7. *Cleidodiscus bedardi* Mizelle, 1936, from *Xenotis megalotis* (Rafinesque).

8. *Cleidodiscus floridanus* Mueller, 1936, from *Ictalurus punctatus* (Rafinesque).

9. *Cleidodiscus pricei* Mueller, 1936, from *Ictalurus punctatus* (Rafinesque), *Ameiurus natalis* (Le Sueur), *Ameiurus nebulosus* (Le Sueur), and *Ameiurus melas* (Rafinesque).

10. *Cleidodiscus nematocirrus* Mueller, 1937, from *Eupomotis gibbosus* (Linnaeus).

11. *Cleidodiscus mirabilis* Mueller, 1937, from *Leptops olivaris* (Rafinesque).

12. *Cleidodiscus stentor* Mueller, 1937, from *Ambloplites rupestris* (Rafinesque).

13. *Cleidodiscus brachus* Mueller, 1938, from *Semotilus atromaculatus* (Mitchill) and *Margariscus margarita* (Cope).

14. *Cleidodiscus alatus* Mueller, 1938, from *Ambloplites rupestris* (Rafinesque).

15. *Cleidodiscus diversus* Mizelle, 1938, from *Apomotis cyanellus* (Rafinesque).

Genus *Urocleidus* Mueller, 1934

Synonyms.—*Onchocleidus* Mueller, 1936, in part; *Tetracleidus* Mueller, 1936, in part; 1936, in part; *Aristocleidus* Mueller, 1936, in part; *Haplocleidus* Mueller, 1937, part; and *Pterocleidus* Mueller, 1937, in part.

Diagnosis (herewith emended).—Tetraonchinae. Body form, eyes, gut, gonads, vitellaria, and bars as described for *Cleidodiscus*. Cirrus a chitinized tube, sometimes straight or undulate with or without a cirral thread or fin, sometimes corkscrew-like. Accessory piece present or lacking—when present, *never basally articulate* with the cirrus. Vagina, when present, opening on the

right margin near middle of body. Haptor generally distinct, subhexagonal; armed with 4 anchors and 14 hooks. The anchors, one pair dorsal and the other ventral. Parasitic on gills of fresh-water fish.

Type species.—Urocleidus aculeatus (Van Cleave and Mueller, 1932) Mueller, 1934.

In *Urocleidus* as defined by Mueller (1934, 1936a) a vagina is lacking. We feel that the absence of a vagina is not of sufficient importance to separate the original species of *Urocleidus* from the dextrally vaginate species now being added to the genus.

Onchocleidus was distinguished (Mueller, 1936a) from *Urocleidus* "in lacking the accessory piece" and "in the presence of a vagina." Price (1937b) describes *Onchocleidus* as "usually with immovable accessory piece." Furthermore, in 3 species described by Mueller (1936a), namely, *O. similis, O. dispar,* and *O. mimus,* and in *O. interruptus* Mizelle, 1936, a vagina was not located.

Tetracleidus was distinguished (Mueller, 1936a) "from *Onchocleidus* in having an accessory piece in the cirrus complex." As pointed out above, this structure is almost always reported for species of *Onchocleidus.*

The principal distinctive features of *Aristocleidus* Mueller, 1936, *Haplocleidus* Mueller, 1936, and *Pterocleidus* Mueller, 1937, are found in the character of the anchors. In *Aristocleidus* the dorsals differ considerably in size and shape from the ventrals. In *Haplocleidus* the dorsals are similar in shape to, but much larger than the ventrals. In *Pterocleidus* the anchors are similar in shape and size but have spurred shafts. We do not consider these variations in the character of the anchors to be of generic significance.

The genus *Urocleidus* as here redefined includes 25 North American and 3 European species. The European forms, placed originally in the genus *Ancyrocephalus* and transferred to *Haplocleidus* by Price (1937b), now become *Urocleidus siluri* (Zandt, 1924) nobis, *Urocleidus monticellii* (Cognetti de Martiis, 1925) nobis, and *Urocleidus vistulensis* (Siwak, 1932) nobis.

KEY TO THE NORTH AMERICAN SPECIES OF UROCLEIDUS

1. Dorsal anchors markedly larger than the ventrals ---------- 2
   Anchors approximately uniform in size ---------- 4
2. Cirrus corkscrew-like ---------- *U. affinis*
   Cirrus, a straight tube ---------- 3
3. Cirrus "about 0.025 mm." long ---------- *U. dispar*
   Cirrus "0.049 mm. long" ---------- *U. furcatus*
4. Each anchor shaft with a distal spur-like projection ---------- 5
   Anchor shafts without spur-like projections ---------- 7
5. Cirrus corkscrew-like ---------- *U. acuminatus*
   Cirrus not corkscrew-like ---------- 6
6. Cirrus with a spiral fin, accessory piece lacking ---------- *U. acer*
   Cirrus with a spiral thread, accessory piece present ---------- *U. biramosus*
7. Bases of ventral anchors deeply bifurcate with distal ends of superficial roots bent toward deep roots; dorsal anchors larger with bases nonbifurcate *U. hastatus*

Ventral and dorsal anchors similar in shape 8
8. Cirrus corkscrew-like 9
Cirrus not corkscrew-like (undulate or straight) 10
9. Proximal portion of each hook differentiated into base and shaft..*U. principalis*
Proximal portions of hooks not differentiated ..... *U. helicis*
10. Cirrus without a thread 11
Cirrus with a spiral thread or "fin" 17
11. Vagina absent 12
Vagina present 15
12. Accessory piece lacking ..... *U. angularis*
Accessory piece present 13
13. Accessory piece terminating in a hook ..... *U. aculeatus*
Accessory piece not hooked 14
14. Bars markedly dissimilar in shape ..... *U. umbraensis*
Bars similar in shape ..... *U. adspectus*
15. Accessory piece apparently lacking ..... *U. ferox*
Accessory piece distinct 16
16. Accessory piece broad, plate-like, not bent distally..... *U. perdix*
Accessory piece slender, elongate, bent at distal tip ..... *U. banghami*
17. Distal end of anchor shafts enlarged ..... *U. distinctus*
Distal end of anchor shafts not enlarged 18
18. Ventral bar with a posteromedial concavity ..... *U. interruptus*
Ventral bar without posteromedial concavity 19
19. Distal end of cirrus flared ..... *U. chautauquaensis*
Distal end of cirrus not flared 20
20. Cirrus with a narrow spiral "fin . . . expanding near its tip" ..... *U. similis*
Cirrus without a distally expanded fin 21
21. Hooks Nos. 1 and 2 smaller than others ..... *U. mimus*
Hooks Nos. 1 and 2 not smaller than others 22
22. Accessory piece vestigial ..... *U. cyanellus*
Accessory piece prominent 23
23. Dorsal bar distinctly larger than the ventral ..... *U. malleus*
Dorsal and ventral bars approximately equal 24
24. Accessory piece "cylindrical" ..... *U. spiralis*
Accessory piece plate-like with a terminal "key-hole effect"..... *U. mucronatus*

North American Species of *Urocleidus*

1. *Urocleidus aculeatus* (Van Cleave and Mueller, 1932) Mueller, 1934. Synonym.—*Ancyrocephalus aculeatus* Van Cleave and Mueller, 1932. Host—*Stizostedion vitreum* (Mitchill).

2. *Urocleidus ferox* Mueller, 1934. Synonym—*Onchocleidus ferox* (Mueller, 1934) Mueller, 1936. Host—*Eupomotis gibbosus* (Linnaeus).

3. *Urocleidus angularis* Mueller, 1934. Synonym—*Ancyrocephalus angularis* (Mueller, 1934) Mueller, 1936. Host—*Fundulus diaphanus menona* (Jordan and Copeland).

4. *Urocleidus adspectus* Mueller, 1936, from *Perca flavescens* (Mitchill).

5. *Urocleidus similis* (Mueller, 1936) nobis. Synonym—*Onchocleidus similis* Mueller, 1936. Host—*Eupomotis gibbosus* (Linnaeus).

6. *Urocleidus mimus* (Mueller, 1936) nobis. Synonym—*Onchocleidus mimus* Mueller, 1936. Hosts—*Lepibema chrysops* (Rafinesque) and (?) *Esox reticulatus* Le Sueur.

7. *Urocleidus helicis* (Mueller, 1936) nobis. Synonym—*Onchocleidus helicis* Mueller, 1936. Host—*Micropterus salmoides* (Lacépède).

8. *Urocleidus acer* (Mueller, 1936) nobis. Synonyms—*Onchocleidus acer* Mueller, 1936, and *Pterocleidus acer* (Mueller, 1936) Mueller, 1937. Hosts—*Eupomotis gibbosus* (Linnaeus) and *Helioperca macrochira* (Rafinesque).

9. *Urocleidus dispar* (Mueller, 1936) nobis. Synonyms—*Onchocleidus dispar* Mueller, 1936, and *Haplocleidus dispar* (Mueller, 1936) Mueller, 1937. Hosts—*Eupomotis gibbosus* (Linnaeus) and *Helioperca macrochira* (Rafinesque).

10. *Urocleidus banghami* (Mueller, 1936) nobis. Synonym—*Tetracleidus banghami* Mueller, 1936. Host—*Micropterus dolomieu* Lacépède.

11. *Urocleidus principalis* (Mizelle, 1936) nobis. Synonym—*Onchocleidus principalis* Mizelle, 1936, and *Onchocleidus contortus* Mueller, 1937 (see Mizelle, 1938b). Hosts—*Micropterus pseudaplites* Hubbs, *Micropterus dolomieu* Lacépède, and *Micropterus salmoides* (Lacépède).

12. *Urocleidus interruptus* (Mizelle, 1936) nobis. Synonym—*Onchocleidus interruptus* Mizelle, 1936. Host—*Morone interrupta* Gill.

13. *Urocleidus mucronatus* (Mizelle, 1936) nobis. Synonym—*Onchocleidus mucronatus* Mizelle, 1936. Hosts—*Helioperca macrochira* (Rafinesque), *Allotis humilis* (Girard), *Eupomotis gibbosus* (Linnaeus) and certain hybrids (Mizelle, 1936).

14. *Urocleidus acuminatus* (Mizelle, 1936) nobis. Synonyms—*Onchocleidus acuminatus* Mizelle, 1936, and *Pterocleidus acuminatus* (Mizelle, 1936) Mueller, 1937. Host *Xenotis megalotis* (Rafinesque).

15. *Urocleidus distinctus* (Mizelle, 1936) nobis. Synonym—*Onchocleidus distinctus* Mizelle, 1936. Host—*Xenotis megalotis* (Rafinesque).

16. *Urocleidus hastatus* (Mueller, 1936) nobis. Synonym—*Aristocleidus hastatus* Mueller, 1936. Host— *Roccus lineatus* (Bloch).

17. *Urocleidus perdix* (Mueller, 1937) nobis. Synonym—*Onchocleidus perdix* Mueller, 1937. Host—*Helioperca macrochira* (Rafinesque).

18. *Urocleidus spiralis* (Mueller, 1937) nobis. Synonym—*Onchocleidus spiralis* Mueller, 1937. Host—*Eupomotis gibbosus* (Linnaeus).

19. *Urocleidus affinis* (Mueller, 1937) nobis. Synonym—*Haplocleidus affinis* Mueller, 1937. Host—*Eupomotis gibbosus* (Linnaeus).

20. *Urocleidus furcatus* (Mueller, 1937) nobis. Synonym—*Haplocleidus furcatus* Mueller, 1937. Host—*Micropterus salmoides* (Lacépède).

21. *Urocleidus biramosus* (Mueller, 1937) nobis. Synonym—*Pterocleidus biramosus* Mueller, 1937. Host—*Helioperca macrochira* (Rafinesque).

22. *Urocleidus malleus* (Mueller, 1938) nobis. Synonym—*Cleidodiscus malleus* Mueller, 1938. Hosts—*Percina caprodes* (Rafinesque) and *Hadropterus maculatus* (Girard). Reasons for transferring this species from *Cleidodiscus* are discussed above in connection with *Cleidodiscus*.

23. *Urocleidus chautauquaensis* (Mueller, 1938) nobis. Synonyms—*Tetracleidus chautauquaensis* Mueller, 1938, and *Cleidodiscus chautauquaensis* (Mueller, 1938) Mueller, 1938—the latter name, found in the explanation of figures in the original description, was evidently used unintentionally. Host—*Ambloplites rupestris* (Rafinesque). This form was described originally as having the vagina on the left side whereas it is actually dextral.*

24. *Urocleidus umbraensis* Mizelle, 1938, from *Fundulus notatus* (Rafinesque).

25. *Urocleidus cyanellus* (Mizelle, 1938) nobis. Synonym—*Onchocleidus cyanellus* Mizelle, 1938. Host—*Apomotis cyanellus* (Rafinesque).

Genus *Actinocleidus* Mueller, 1937

Diagnosis.—Body form, eyes, gut, gonads, cirrus, accessory piece, vagina, and vitellaria as in *Cleidodiscus*. Haptor, distinct and discoidal; armed with 4 anchors and 14 hooks. Anchors, both pairs ventral, approximately uniform in size and shape, bases of each pair connected by a transverse bar; bars articulate. Parasitic on gills of fresh-water fish.

Type species.—*Actinocleidus oculatus* (Mueller, 1934) Mueller, 1936.

Species of *Actinocleidus* have thus far been reported only from North America.

Key to the Species of Actinocleidus

1. Base and shaft of each anchor united as a single large triangular plate ..... *A. triangularis*
   Bases and shafts of anchors distinct 2
2. Accessory piece aviform ..... *A. articularis*
   Accessory piece not aviform 3
3. Accessory piece with a knob-like process near the middle 4
   Accessory piece without a knob 5
4. Cirrus sickle-shaped ..... *A. fergusoni*
   Cirrus undulate ..... *A. gracilis*

* Pursuant to inquiry by one of us (Mizelle) Dr. J. F. Mueller requested Dr. E. W. Price to re-examine the type material in the United States National Museum—the vagina was found to be dextral. This information occurs in a personal letter (March 22, 1938) from Dr. Price to Dr. Mueller, which was kindly forwarded to us.

5. *Accessory piece whip-like* ---------- *A. longus*
   Accessory piece not whip-like ---------- 6
6. Cirrus S-shaped ---------- 7
   Cirrus not S-shaped ---------- 8
7. Base of accessory piece hooked ---------- *A. bursatus*
   Base of accessory piece not hooked ---------- *A. maculatus*
8. Base of accessory piece bifurcate ---------- *A. oculatus*
   Base of accessory piece not bifurcate ---------- *A. fusiformis*

Species of *Actinocleidus*

1. *Actinocleidus fusiformis* (Mueller, 1934) Mueller, 1937. Synonym—*Cleidodiscus fusiformis* Mueller, 1934. This is perhaps the same species as the form identified by Cooper (1915) as "*Ancyrocephalus cruciatus* (Wedl)." Hosts—*Micropterus dolomieu* Lacépède and *Micropterus salmoides* (Lacépède).

2. *Actinocleidus oculatus* (Mueller, 1934) Mueller, 1937. Synonym—*Cleidodiscus oculatus* Mueller, 1934. Host—*Eupomotis gibbosus* (Linnaeus).

3. *Actinocleidus bursatus* (Mueller, 1936) Mueller, 1937. Synonym—*Ancyrocephalus bursatus* Mueller, 1936. Host—*Micropterus salmoides* (Lacépède).

4. *Actinocleidus articularis* (Mizelle, 1936) Mueller, 1937. Synonym—*Cleidodiscus articularis* Mizelle, 1936. Host—*Xenotis megalotis* (Rafinesque).

5. *Actinocleidus gracilis* Mueller, 1937, from *Helioperca macrochira* (Rafinesque).

6. *Actinocleidus maculatus* Mueller, 1937, from *Eupomotis gibbosus* (Linnaeus).

7. *Actinocleidus triangularis* Summers, 1937, from *Lepomis symmetricus* Forbes.

8. *Actinocleidus longus* Mizelle, 1938, from *Apomotis cyanellus* (Rafinesque).

9. *Actinocleidus fergusoni* Mizelle, 1938, from *Helioperca macrochira* (Rafinesque).

Genus *Murraytrema* Price, 1937

Diagnosis (quoted from Price, 1937b).—"Cephalic glands opening to exterior through 4 pairs of head organs. Haptor large, with 2 pairs of large hooks separated by 3 transversely placed nonarticulate bars; 14 marginal hooklets. Intestinal branches not uniting posteriorly. Eyes present. Testis and ovary in equatorial zone. Cirrus with accessory piece. Vagina present, opening ventrally and medially."

Type species.—*Murraytrema robusta* (Murray, 1931) Price, 1937.

This genus includes two species, (1) *M. robusta* in Australia described

by Murray (1931) as *Ancyrocephalus robusta*, and (2) *Murraytrema copulata* Mueller, 1938, from *Castostomus commersonii* (Lacépède), *Hypentelium nigricans* (Le Seur), *Moxostoma anisurum* (Rafinesque), and *Moxostoma erythrurum* (Rafinesque) in this country.

REFERENCES

Cognetti de Martiis, L. 1925—Nuovo gyrodactylide parassita nella cavita olfattiva di *Ameiurus catus* L. Boll. Soc. d. nat. in Napoli, 1924, 36(s. 2), **16**(anno 38):76-81.

Cooper, A. R. 1915—Trematodes from marine and fresh-water fishes, including one species of ectoparasitic turbellarian. Trans. Roy. Soc. Canada (Ottawa), Sect. 4, 3. s., **9**:181-205.

Johnston, T. H. and O. W. 1922—New gyrodactylid trematodes from Australian fishes, together with a reclassification of the superfamily Gyrodactyloidea. Proc. Linn. Soc. N. South Wales, Sydney, (186), **47**(2):83-131.

Mizelle, J. D. 1936—New species of trematodes from the gills of Illinois fishes. Amer. Midl. Nat. **17**(5):785-806.

———1937—Ectoparasites of the blunt-nosed minnow *(Hyborhynchus notatus)*. Ibid. **18**(4):612-621.

———1938a—New species of monogenetic flukes from Illinois fishes. Ibid. **19**(2): 465-470.

———1938b—Comparative studies on trematodes (Gyrodactyloidea) from the gills of North American fresh-water fishes. Ill. Biol. Monogr. **17**(1): in press.

Mueller, J. F. 1934—(Parasites of Oneida Lake fishes). Part IV. Additional notes on parasites of Oneida Lake fishes, including descriptions of new species. Roosevelt Wild Life Ann. **3**(4):335-373.

———1936a—Studies on North American Gyrodactyloidea. Trans Amer. Micro. Soc. **55**(1):55-72.

———1936b—New gyrodactyloid trematodes from North American fishes. Ibid. **55**(4):457-464.

———1937—Further studies on North American Gyrodactyloidea. Amer. Midl. Nat. **18**(2):207-219.

———1938—Additional species of North American Gyrodactyloidea (Trematoda). Ibid. **19**(1):220-235.

Murray, F. V. 1931—Gill trematodes from some Australian fishes. Parasitol. **23**(4):492-506.

Price, E. W. 1934—A new term for the adhesive organs of trematodes. Proc. Helminth. Soc. Wash. **1**(2):34.

———1937a—A new monogenetic trematode from Alaskan salmoid fishes. Ibid. **4**(1):27-29.

———1937b—North American monogenetic trematodes. I. The super-family Gyrodactyloidea. Jour. Wash. Acad. Sci. **27**(3):114-130, and (4):146-164.

———1938—The monogenetic trematodes of Latin America. In Livro Jubilar Prof. Travassos. Rio de Janeiro, Brasil. **3**:407-413.

SEAMSTER, A. 1938—Studies on gill trematodes from Oklahoma fishes. Amer. Midl. Nat. **20**:(in press).

SIWAK, J. 1932—*Ancyrocephalus vistulensis* sp. n., nowy gatunek przywry, pasorzytujacy na sumie (*Silurus glanis* L.).—*Ancyrocephalus vistulensis* sp. n., un nouveau trematode, parasite du silure (*Silurus glanis* L.). Bull. Internat. Acad. Polon. Sci. et Lettres, Cracovie, Cl. Sci. Math. et nat., s. B: Sc. Nat. (II), (7-10):669-679.

STAFFORD, J. 1905—Trematodes from Canadian vertebrates. Zool. Anz. **28**(21-22): 681-694.

SUMMERS, W. A. 1937—A new species of Tetraonchinae from *Lepomis symmetricus*. Jour. Parasitol. **23**(4):432-434.

VAN CLEAVE, H. J. AND J. F. MUELLER. 1932—Parasites of Oneida Lake fishes. Part I. Descriptions of new genera and new species. Roosevelt Wild Life Ann. **3**(1):9-71.

———1934—Ibid. Part III. A biological and ecological survey of the worm parasites. Ibid. **3**(3):161-334.

WEGENER, G. 1910—Die Ektoparasiten der Fische Ostpreussens. Schrift. phys.-ökonom. Ges. Königsberg **50**(3):195-286.

ZANDT, F. 1924—Fischparasiten des Bodensees. Centralb. Bakteriol., Parasitenk. u. Infectionskrankh., I. Abt. **92**(3-4):225-271.

Nine New Thysanoptera from North America

J. Douglas Hood

The insects described in the following pages are almost without exception members of genera in which taxonomic separation is difficult; and for this reason several are represented by odd slides which have reposed in corners of slide-boxes for many years. The opportunity to study certain European types, and to see several American ones which had long been inaccessible, has finally permitted tentative revisions of the genera concerned. It has appeared worth while to publish the new names at the present time.

One or more of the tubuliferous species may have been previously described in genera to which they do not belong; but the hope of examining and satisfactorily studying all of the pertinent types, scattered as they are, and of arriving at conclusions which are not likely to be considerably modified by the study of properly mounted material, has become too remote to warrant further postponement of publication.

The types of the new species are in the author's collection.

Æolothrips pallidicornis sp. nov.

Female (macropterous).—Length about 1.6 mm. (fully distended, nearly 2.0 mm.). Color blackish brown, with a reddish cast due to the presence of bright red internal pigmentation in head, thorax, abdomen, femora, and first two antennal segments; antennae about concolorous with head in segments I and II, the latter segment yellowish medially at apex, III and IV yellowish white, the former often with the extreme tip slightly darkened with brown, the latter lightly brownish in distal third or more,[1] V-IX pale grayish-brown; legs blackish brown, tarsi not lighter; fore wings with a dark, nearly black, longitudinal vitta occupying the entire posterior half (including scale), this vitta not at all broadened near middle of wing to form a partial cross-band, the anterior half of wing colorless, with white[1] veins.

Head with its length about equal to greatest width across cheeks, which is just perceptibly greater than the width across eyes, entire dorsal surface behind ocelli distinctly and rather closely sculptured with transverse dark lines, and with the usual minute setae on occiput and cheeks; cheeks moderately arched. Eyes about 0.4 as long as head, in holotype with dorsal length 77μ, dorsal width 54μ, and dorsal interval 78μ; ventral surface prolonged posteriorly. Ocelli large, the median one 23μ in diameter and 22μ from the posterior ones, which are 20μ in diameter and 36μ apart (holotype). Antennae normal

[1] By transmitted light segments III and IV of the antennae and the veins in the anterior portion of the fore wings often appear much darker in specimens which have been in preservative for only a short time and in which, therefore, the white "pigment" has not been destroyed.

except that segment V is nearly or fully as long as IV and about 1.6 times as long as VI-IX together; sense-area on III elongated, about 39μ long (31-44μ), that on IV broadened distally and about 36μ long (32-42μ), that on IV broadened distally and about 36μ long (32-42μ); sense-cone on V arising at about distal third of segment and attached at base only, the pale spot nearly circular. (Maxillary palpi three-segmented).

Prothorax along median line of pronotum about two-thirds as long as greatest width, distinctly broadeer than head, its surface distinctly and rather closely cross-striate. Mesothorax about 1.5 times as broad as prothorax, of the usual form; mesonotum sculptured like head and pronotum; metanotum with the usual subreticulation. Wings of fore pair about 7.6 times as long as greatest width, which is beyond middle; venation normal. Legs normal.

Abdomen of the usual form and structure; tergum I subreticulate, more strongly near base; abdominal terga VII-X medially 98, 100, 132, and 114μ in holotype; tergum IX with seta I 140μ, II 150μ, III 139μ; tergum X with seta I 142μ, II 152μ.

Measurements of female (holotype), in mm.: Length about 1.64 (distended, 1.95); head, length 0.189, width across eyes 0.186, greatest width across cheeks 0.188, least width near base (in front of basal collar) 0.176; prothorax, median length of pronotum 0.146, greatest width (exclusive of coxae) 0.218; mesothorax, greatest width 0.330; metathorax, greatest width 0.298; fore wings, length 1.06, greatest width (beyond middle) 0.136; abdomen, greatest width 0.403.

Antennal segments.	1	2	3	4	5	6	7	8	9	
Length (μ):	35	58	115	84	90	16	13	13	12	(holotype)
	35	59	121	94	84	14	13	12	13	(paratype)
Width (μ):	36	31	26	26	27	19	15	11	7	(holotype)
	40	31	26	26	26	19	16	11	7	(paratype)

Total length of antenna, holotype 0.436, paratype 0.445 mm.

NEW YORK: Oswegatchie, J. D. H.; 4 ♀♀ on dying branches and leaves of *Abies balsamea* (June 14 and 18, 1936), 1 ♀ by sweeping (September 5, 1936).

From the other species of *Æolothrips* in which the dark color on the fore wings is confined wholly to the posterior half of the wing and in which this dark vitta extends to the very base, *pallidicornis* may readily be known by the elongated fifth antennal segment and the rather pale antennae.

Chirothrips lenape sp. nov.

Female (macropterous).—Length about 1.12 mm. Color brown, somewhat paler than *C. manicatus*, with orange internal pigmentation in thorax and abdomen, legs about concolorous with body, the fore tibiæ lighter in distal half and somewhat yellowish at apex, all tarsi yellow, the middle and hind pairs lightly shaded with brownish; fore wings brown, paler subbasally, with a small colorless spot distal to scale, darker apically and in distal half of posterior margin, veins distinctly shaded to beyond fork; antennæ with segment

I concolorous with head and IV-VIII uniform dark grayish brown, II palest, yellowish brown in color, and very darkly but narrowly shaded across base, along inner surface, and in basal half of outer surface, III just perceptibly paler than IV-VIII, the basal part of its pedicel yellowish.

Head with its total median length a trifle greater than its greatest width (which is across eyes) and about 0.6 as long as pronotum, distinctly produced (9-10μ) in front of eyes, the sides of this production very slightly converging posteriorly, surface of head without distinct striæ behind posterior ocelli, frontal costa moderately narrow and slightly notched; vertex normally with three pairs of small setæ, of which two are nearly equally spaced and on almost the same transverse line immediately behind the bases of antennæ, the other directly behind the middle pair just mentioned and about the same distance apart, this distance being approximately that between the interocellar setæ; interocellars small and on the same transverse line as front margin of median ocellus; occiput with the usual three pairs of setæ just behind eyes and a similar lateral pair in the same series. Eyes moderate in size, almost exactly half the length of head, in holotype with dorsal length 55μ, dorsal width 30μ, and dorsal interval 45μ. Ocelli normal, the median one smaller, about 8μ in diameter and 63μ from anterior end of head, the posterior pair about 10μ in diameter, 31μ apart, and 14μ from median ocellus. Antennæ normal; segment I enlarged, rounded, and often with a transverse carina, its length about equal to that of II and of III; II considerably produced at apex, distinctly concave in outer surface, and with a rather prominent, stout, sense-cone-like seta at tip of process, this seta curved abruptly forward, the median length of this segment 29μ, length of outer surface 38-41μ, maximum diagonal length 47-49μ, distance from tip of projection to pedicel of III, 20-22μ; III and IV normal, each with a stout simple sense-cone; V unusual in that the sense-cone on outer surface is moderately long (10μ). Mouth-cone typical, broadly rounded, its length beyond posterior dorsal margin of head about 82μ.

Prothorax about 1.44 times as broad as long and 1.6-1.7 times as long as head; pronotum with the lines of sculpture relatively weak, not regularly interrupted or broken into scallops; setæ at posterior angles of pronotum short, only 21-27μ. Pterothorax normal; metascutum with the mediad pair of setæ short, stout, and situated distinctly (14μ) posterior to the lateral pair; metascutellum 3.4-4 times as wide as long; mesosternum with the sculpture in the region of the lateral angles more or less broken into faint scallops. Legs normal; fore femora weakly sculptured, their anterior dorsal margin not reflexed. Wings nearly straight, the fore pair with 4 + 3 setæ near base of anterior vein and 1 + 1 in distal third of wing, the posterior vein with 3 or 4.

Abdomen broad and heavy, nearly 1.4 times as wide as prothorax, with the usual distinct dark lines of sculpture on dorsal surface; subbasal chitinous line on terga (including I and II) not broken into dark dashes or scallops; posterior margins of terga produced into a thin lobulate flange, of sterna into short, thickened scallops which extend entirely across sternum II, nearly disappear in about median third of III, and are present only at sides of

IV-VI; ventral sculpture weak, that of sterna II and III largely broken into weak scallops which, however, do not form a heavy prominent submarginal row; segment X not elongated or acute, its length about 83μ, its greatest subbasal width 73μ; setæ pale brownish, normal in disposition, segment IX with setæ 1-3 about 80μ long, and X with 1 and 2 about 108 and 98μ, respectively.

Measurements of female, in mm.[2]: Length about 1.12; head, total length 0.107 (0.103), width across eyes 0.105 (0.099), greatest width across cheeks 0.104 (0.097), length in front of eyes 0.036 (0.034), lateral length of head-process 0.010 (0.009), length of cheeks 0.018 (0.016), greatest width of head-process 0.073 (0.069), least interval between bases of antennæ 0.007 (0.005); prothorax, median length of pronotum 0.182 (0.168), greatest width 0.262 (0.245), width across anterior margin 0.117 (0.110); mesothorax, greatest width 0.322; metathorax, greatest width 0.286; metascutellum, greatest width 0.141 (0.144), median length 0.041 (0.033); fore wings, length 0.742, width at middle 0.043; abdomen, greatest width 0.360.

Antennal segments:	1	2	3	4	5	6	7	8
Length (μ):	28	29	29	34	29	36	11	9
Width (μ):	46	--	26	26	23	19	7	4

Total length of antenna 0.205 mm.

NEW JERSEY: Leonia, May 13, 1916, E. R. Kalmbach, from sedges and cattails in marsh, 2 ♀♀.

Though resembling *C. manicatus* so closely as to be easily confused with it, this species differs in a multitude of details, all of which have been described above. Perhaps the most outstanding characters are the presence of a large, stout, recurved seta at the tip of the second antennal segment, the large sense-cone on the outer surface of the fifth, the less strongly sculptured occiput, the short prothoracic setæ, and the very different sculpture of the ventral surface.

Chirothrips orizaba sp. nov.

Female (macropterous).—Length about 1.45 mm. (fully distended, 1.76 mm.). Color dark brown or blackish brown, with tips of fore tibiæ paler and all tarsi nearly or quite yellow; fore wings brown; antennæ with segments I and II about concolorous with head, II somewhat paler distally and medially, IV-VIII uniform dark grayish brown, III paler.

Head with its total median length about equal to its greatest width (the distance across eyes and across cheeks about equal) and nearly 0.6 as long as pronotum, distinctly produced (14μ) in front of eyes, the sides of this process straight and very slightly converging to its sharp anterior angles, surface of head with several distinct striæ behind posterior ocelli, frontal costa moderately narrow and slightly notched, interval between antennal bases about 8μ; vertex with three pairs of setæ in advance of interocellars, the most lateral pair situated in anterior angles of head-process, another pair on a line

[2] Measurements in parentheses, when given, are of the paratype, while all others are of the holotype.

with anterior margins of eyes and 63μ apart in the unique type, the remaining pair 3-7μ in advance of eyes and 33μ apart; interocellar setae 45μ apart and 11μ in advance of anterior margin of median ocellus; occiput with the usual three pairs of setæ just behind eyes and a similar lateral pair in the same series. Eyes moderate in size, a trifle more than half the length of head; their dorsal length 62μ, dorsal width 33μ, dorsal interval 56μ. Ocelli normal, the median one smaller, about 9μ in diameter and 69μ from anterior end of head, the posterior pair about 11μ in diameter, 33μ apart, and 17μ from median ocellus. Antennæ normal; segment I not enlarged but quite rounded, its length much less than that of segment II; II produced as usual at apex, its outer surface very slightly concave, the apex of production acute and without a minute terminal seta, the median length of this segment 30μ, length of outer surface 33μ, maximum diagonal length 44μ, distance from tip of projection to pedicel of III, 17μ; sense-cones simple, that on outer surface of apex of V only 5μ. Mouth-cone typical, broadly rounded, its length beyond posterior dorsal margin of head about 105μ.

Prothorax about 1.23 times as broad as long and 1.7 times as long as head; pronotum with the lines of sculpture dark and moderately strong, showing little tendency to break into scallops; inner setæ at posterior angles of pronotum 50μ, outer 43μ. Pterothorax normal; metascutum with the usual two pairs of setæ slender, the mediad pair situated about 11μ behind the lateral pair and 30μ apart; metascutellum about 2.4 times as wide as long; mesosternum with its anterior margin deeply (15μ) concave, its sculpture in the region of the lateral and anterior angles broken into faint scallops. Legs normal; fore femora heavily sculptured and with their anterior dorsal margin strongly reflexed. Wings nearly straight, the fore pair with 4 (or 5) + 2 + 1 setæ in basal third of anterior vein and 1 + 1 + 1 beyond, the posterior vein with 6 or 7.

Abdomen normal, scarcely 1.4 times as wide as prothorax, with the usual distinct dark lines of sculpture on dorsal surface; subbasal chitinous line on terga (including I and II) not broken into dark dashes or scallops; posterior margins of terga (excepting I, which is bare) produced into a thin and slightly lobulate flange, of sterna II-V into short dark scallop-like thickenings which are absent from between the median pair of setæ and become fewer, less conspicuous, and more confined to lateral portions on sterna IV and V, VI with perhaps one or two at extreme lateral margin, VII bare; ventral sculpture weak, that of sterna II-VI forming a submarginal dark line which is more or less interrupted and on II distinctly broken into weak scallops; segment X about 95μ long; setæ normal in disposition, segment IX with seta I measuring 102-108μ, II 120μ, and III 142-147μ; X with seta I 137μ, II 134μ.

Measurements of female (holotype), in mm.: Length about 1.45 (fully distended, 1.76); head, total length 0.118, width across eyes 0.121, greatest width across cheeks 0.122, length in front of eyes 0.034, lateral length of head-process 0.014, length of cheeks 0.021, greatest width of head process 0.082; prothorax, median length of pronotum 0.202, greatest width, 0.248, width across anterior margin 0.135; mesothorax, greatest width ca. 0.301; metathorax, greatest width ca. 0.252; metascutellum, greatest width 0.118, length 0.050;

fore wings, length 0.962, width at middle 0.047; abdomen, greatest width 0.343.

Antennal segments:	1	2	3	4	5	6	7	8
Length (μ):	23	30	32	37	29	43	10	13
Width (μ):	36	...	26	26	23	19	7	5

Total length of antenna, 0.217 mm.

MEXICO: Mt. Orizaba, February, 1892, Smith, 1♀, "from seeds of *Epicampes* grass."

The moderately produced head, short first antennal segment, and the lack of a strictly terminal seta at the tip of the process of the second antennal segment, ally this species only with *C. productus* Hood, from which, however, it is readily separated by a number of characters, such as the deeply concave anterior margin of the mesosternum, the much more delicate and very different type of sculpture of the abdominal sterna, and the greater length of the fourth antennal segment in comparison with the fifth.[3]

Anaphothrips tenebrosus sp. nov.

Female (macropterous).—Length about 1.2 mm. (partially distended, 1.3 mm.). Color brown, somewhat darker in abdomen (especially in the last two segments) and distinctly yellowish in thorax and in all of anterior three-fourths of head except the margins; ocellar pigmentation bright red; legs yellow, rather heavily shaded with brown along outer margin of all femora and tibiæ; antennæ with segments I, II, and VI-IX brown, II much darker than I but paler than the distal ones, III-IV brownish yellow, IV somewhat darker than III and narrowly shaded at apex with brown, V brown, apically as dark as VI, basally as light as the paler median portion of II; fore wings light brownish yellow, with darker veins.

Head about 0.85 as long as greatest width, which is across cheeks, and somewhat shorter than pronotum, its cheeks slightly rounded, narrowing rather strongly to eyes and gently to base; dorsal surface sculptured in the darkly colored portions, the striæ producing a distinct serration in the posterior part of cheeks, the vertex with a slight median furrow; cephalic setæ small, most of them 12-13μ long. Eyes about 0.5 as long as head, 62μ in length, about 37μ wide, and about 62μ apart. Ocelli 11-12μ in diameter, the median one with its anterior margin about 6μ behind that of eyes. Antennæ 9-segmented, normal in structure. Mouth-cone normal but large, extending about 130μ beyond posterior dorsal margin of head; maxillary palpi three-segmented.

Prothorax about 1.46 times as wide as long, very lightly sculptured along anterior and posterior margins, without larger setæ on posterior angles, the inner pair on posterior margin perhaps largest and measuring 17-18μ. Pterothorax normal; fore wings about 0.81 mm. long and 57μ wide at middle, setæ colorless and moderately long, those at middle of posterior vein 27μ, costa with about 23, anterior vein with 8 or 9 near base (sometimes 5 + 4 or 4 + 4) and 3 or 4 more or less equally spaced ones in distal two-thirds of wing, posterior vein with 10-11.

[3] In the original description of *C. productus* the length of the fifth antennal segment was incorrectly given as 48μ, instead of 28μ.

Abdomen nearly 1.5 times as broad as prothorax, tergum VIII with complete even comb, the microtrichia composing it broadened basally, the longest about 18μ; segment X divided dorsally nearly to base; distal setæ long and quite slender, IX of holotype with seta I 84μ, II 96μ, X with seta I 76μ, II 67μ; ovipositor 210μ.

Measurements of female (holotype), in mm.: Length about 1.19 (fully distended, 1.29); head, total length 0.122, length to anterior margin of eyes 0.112, width across eyes 0.136, least width just behind eyes 0.132, greatest width across cheeks 0.143; prothorax, median length of pronotum 0.130, greatest width 0.190; mesothorax, greatest width 0.255; abdomen, greatest width 0.283; tergum VII, median length 0.084, VIII 0.083, IX 0.068, X 0.068, greatest subbasal width of X 0.062.

Antennal segments:	1	2	3	4	5	6	7	8	9
Length (μ):	21	33	44	37	38	39	12	11	16
Width (μ):	30	28	20	20	20	18	12	7	5

Total length of antenna 0.251 mm.

NEW JERSEY: Leonia, May 13, 1916, E. R. Kalmbach, 2 ♀♀ (holotype and paratype) taken by sweeping.

DISTRICT OF COLUMBIA: Bennings, Sept. 7, 1913, J. D. H., 2 ♀♀ (paratypes) taken by sweeping.

Allied to *obscurus, cameroni, badius,* and *zizania.* Separable from *obscurus* by the color and longer wing setæ; from *cameroni* by the color, shorter antennal segments, and shorter abdominal setæ; from *badius* by the much paler wings and body; and from *zizania* by the differently proportioned antennal segments.

Anaphothrips zizania sp. nov.

Female (macropterous).—Length about 1.15 mm. (partially distended, 1.29 mm.). Color brown; legs brownish yellow, with femora and tibiæ darkly shaded with brown along outer surface; antennæ with segments I, II, and VI-IX brown, II darkest, III-V brownish yellow, IV somewhat darker than III and narrowly shaded at apex with brown, V brown, apically as dark as VI, basally distinctly yellowish, VI with a narrow pale band just beyond pedicel; fore wings brownish yellow, with darker veins.

Head about 0.84 as long as greatest width, which is across cheeks, and somewhat shorter than pronotum, its cheeks slightly rounded, narrowing rather strongly to eyes and gently to base; dorsal surface sculptured except between eyes, the deeper striæ at sides producing a rather prominent serration in the cheeks; cephalic setae small, most of them 11-12μ long. Eyes about 0.52 as long as head, 64μ in length, about 39μ wide, and about 64μ apart. Median ocellus about 10μ in diameter, its anterior margin about 7μ behind that of eyes; posterior ocelli about 13μ in diameter, 28μ apart, and 20μ from median ocellus. Antennae 9-segmented and normal in structure, except that the segments are unusually stout. Mouth-cone normal, extending about 114μ beyond posterior dorsal margin of head; maxillary palpi three-segmented.

Prothorax about 1.4 times as wide as long, distinctly sculptured along anterior and posterior margins and at sides, without larger setæ on posterior

angles, the inner pair on posterior margin perhaps largest and measuring 17-18μ. Pterothorax normal; fore wings about 0.78 mm. long and 56μ wide at middle, setæ colorless and moderately long, those at middle of posterior vein 35μ, costa with about 29, anterior vein with 4 + 3 near base and 4 in distal two-thirds of wing, the second and third of these about twice as far apart as from the others, posterior vein with 10.

Abdomen about 1.6 times as broad as prothorax, tergum VIII with comb complete but somewhat irregular, the microtrichia composing it broadened basally, the longest about 17 microns; segment X divided dorsally nearly to base; distal setæ long and quite slender, IX of holotype with seta I 78μ, II 74μ, III 83μ, X with seta I 72μ, II 72μ: ovipositor 210μ.

Measurements of female (holotype), in mm.: Length about 1.15 (fully distended, 1.29); head, total length 0.123, length to anterior margin of eyes 0.107, width across eyes 0.143, greatest width across cheeks 0.149; prothorax, median length of pronotum 0.127, greatest width ca. 0.179; mesothorax, greatest width 0.235; abdomen, greatest width 0.288; tergum VII, median length 0.080, VIII 0.086, IX 0.072, X 0.070, greatest subbasal width of X 0.072.

Antennal segments:	1	2	3	4	5	6	7	8	9
Length (μ):	20	34	40	34	36	39	11	10	17
Width (μ):	30	29	22	21	21	20	12	7	5

Total length of antenna 0.241 mm.

Male (brachypterous).—Much smaller than female, with shorter and stouter antennæ (see measurements); color as in female, except that the pterothorax is paler than rest of body. Sterna III-VII each with a glandular area shaped much as in *tersus*, except that the ends are broadened and less turned inward; tergum VIII with comb complete and regular; tergum IX with two pairs of very stout, brown, tooth-like setæ arising from prominent tubercles, the anterior pair 13-14μ long, about 4μ in diameter, and situated above the others, which are 10μ long and about 3μ in diameter; tergum IX also with a pair of slender setæ 47μ long and 46μ apart arising about 6μ in advance of the stouter pair of setæ, and a pair of similar, nearly lateral setæ about 54μ long arising on the same line as the stouter setæ.

Measurements of male (allotype), in mm.: Length about 0.84 (very slightly distended, 0.87); head, length 0.106, width across eyes 0.117, least width just behind eyes 0.115, greatest width across cheeks 0.124; eyes, dorsal length 0.054, width 0.032, interval 0.052; median ocellus, diameter 0.008; posterior ocelli, diameter 0.010, interval 0.024, distance from median ocellus 0.021; mouth-cone, length beyond posterior dorsal margin of head 0.90; prothorax, median length of pronotum 0.092, width 0.151; mesothorax, greatest width 0.170; fore wings, length 0.223; abdomen, greatest width 0.189.

Antennal segments:	1	2	3	4	5	6	7	8	9
Length (μ):	18	30	33	28	31	31	10	10	13
Width (μ):	28	27	21	20	20	18	13	8	5

Total length of antenna 0.204.

MICHIGAN: Cheboygan Co., October 5, 1934, W. Carrington Frohne, 1 ♀ and 1 ♂, "in axils or sheaths of wild rice, Indian River."

Though this species resembles *cameroni, tenebrosus,* and *badius* in coloration, it is readily distinguished by the much stouter antennæ and heavier sculpture. The glandular areas on the abdominal sterna of the male are very different in form from those of *obscurus, cameroni,* and *badius.*

Oxythrips pallidiventris sp. nov.

Female (macropterous).—Length about 1.3 mm. (distended, about 1.5 mm.). General color yellow, head lemon-yellow, pterothorax with an orange cast; abdomen with terga I-VII obscurely shaded with gray across base, prothorax and pterothorax with obscure gray spots also; legs dull yellow, femora and tibiæ (especially the fore and middle pairs) lightly and obscurely shaded with brownish on outer surface; wings of fore pair distinctly gray, the veins perceptibly darker; antennæ with segment I pale yellowish white, II darker and shaded with grayish, III darker than II and more brownish in color, often infuscate apically, IV-VIII dark gray-brown, IV and V paler basally and often narrowly nearly black at apex; ocellar pigmentation bright vermilion red.

Head about 0.9 as long as greatest width, which is across eyes, cheeks tapering to eyes and very slightly narrowed to base, the width at these two points equal; vertex not at all swollen or overhanging, sloping evenly downward, frontal costa with a shallow, V-shaped notch; dorsal surface faintly cross-striate between posterior ocelli and base of head, the cheeks serrate in posterior half; one pair of minute setae (17μ apart) in front of median ocellus, a second similar pair directly laterad of median ocellus and close to inner margins of eyes, an interocellar pair about 17μ long on the edge of the ocellar triangle, three pairs (10μ) near inner posterior margin of eyes (the middle of these more anterior than the others and on a line with posterior margin of eyes), and two pairs at anterior third of cheeks, all of these setae colorless. Eyes about 0.5 the length of head, somewhat protruding, their dorsal length 60-63μ. Ocelli of posterior pair situated distinctly behind middle of eyes. Antennæ of perfectly normal structure, though longer and more slender than usual; segment III about 44μ long; VI without subapical, transverse, ventral suture.

Prothorax usually nearly equal in length to head and 1.5 times as wide as long; dorsal surface faintly cross-striate; major seta at posterior angles pale yellow and 27-37μ long; posterior margin with four pairs of setæ between the major pair, the innermost of these about 16μ and slightly longer than the others. Legs normal in structure; fore tarsus not toothed. Wings of fore pair with about 27 grayish yellow setæ on costal margin, those at middle of wing about 25μ; fore vein with 4 + 4 in basal third, 1 at middle, and 2 near tip; hind vein with about 7 nearly equally spaced ones.

Abdomen of normal form and structure; setæ on tergum IX yellow, normal in structure (i. e., not as in *O. flavus*), the dorsal pair about 76μ, dorso-lateral 82μ, lateral 73; X not elongate or tubiform, its dorsal setæ about 73μ, dorso-laterals 66μ; tergum VIII without comb.

Measurements of female (holotype), in mm.: Length about 1.32 (fully

distended, 1.52); head, length 0.122, width across eyes 0.133, least width just behind eyes 0.127, greatest width across cheeks 0.132, least width near base 0.127; prothorax, median length of pronotum 0.110, greatest width 0.167; mesothorax, greatest width 0.224; fore wings, length 0.697, width at middle 0.050; abdomen, greatest width (at segment IV) 0.274; segment X, length 0.070, greatest subbasal width 0.075.

Antennal segments:	1	2	3	4	5	6	7	8
Length (μ):	20	38	44	39	35	49	10	17
Width (μ):	28	25	21	20	19	19	7	5

Total length 0.252 mm.

FLORIDA: Dunedin, December 22, 1937, Dr. J. Chester Bradley and J. D. H., 15 ♀♀ from flowers of a short-leaved pine [Hood No. 1326].

This species is a close relative of *pinicola,* but aside from the paler coloration, especially of the abdomen, it may be easily recognized by the more slender head and shorter setæ.

Karnyothrips brimleyi sp. nov.

Female (macropterous).—Length about 1.3 mm. (fully distended 1.7 mm.). Color blackish brown, head somewhat darker than thorax; legs concolorous with body, with all tarsi and tips of fore and hind tibiae paler but scarcely yellow; antennae with segments I and II blackish brown, I paler across base, II with median apical portion somewhat paler and with inner and outer surfaces and base nearly black, III-VIII uniform blackish brown except for the yellow basal third of III; fore wings brown in scale and to the last subbasal seta, and with a slight brownish cloud in middle third; internal pigmentation bright crimson.

Head about 1.32 times as long as greatest width (which is at about anterior third of cheeks), distinctly though slightly notched at posterior angles of eyes; cheeks rounded, slightly narrowed toward eyes and somewhat more distinctly to a very short parallel-sided basal portion; dorsal surface smooth and shining, free of sculpture save for two or three lateral striae just in front of the usual subbasal line; vertex slightly overhanging and bearing the forwardly-directed median ocellus at its extremity; postocular setae pale yellowish, slender, and slightly dilated at apex, their length about 25μ, interval 98μ, distance from eyes 19μ. Eyes slightly protruding and thus not evenly rounded with curve of head, about 53μ long. Ocelli about 13μ in diameter, the posterior pair about 31μ apart and 20μ from median ocellus. Antennæ moderately stout, thoroughly typical, segment VIII nearly conical and broadly attached to VII, with a slight constriction just beyond base; sense-cones slender and very inconspicuous, arranged as follows on inner (and outer) surfaces of segments: III 1(1), IV 1(2), V 1(1 + 1), VI 1(+1), VII 1 dorsal. Mouth-cone typical, extending about 77μ beyond posterior dorsal margin of head.

Prothorax with median length of pronotum about 0.63 that of head and contained in the trans-coxal width about twice, with short median thickening

at middle, surface perfectly smooth save for one or two cross-striae along posterior margin; antero-marginal setæ very minute (about 6μ) and pointed, the others pale yellowish and dilated apically, antero-angulars about 20μ, midlaterals 18μ, epimerals 42μ, postero-marginals 29μ, coxals 24μ. Pterothorax across anterior angles somewhat narrower than prothorax across coxae. Legs typical, fore femora slightly enlarged, fore tarsi with the usual tooth at apex of inner surface of first segment. Fore wings about 0.644 mm. long, thoroughly typical, usually with 3 (occasionally 2 or 4) accessory setæ, and with the subbasal setæ (in holotype) respectively 20, 20, and 25μ.

Abdomen of normal form and structure, wider than prothorax, its major setæ pale yellowish brown and distinctly dilated apically, excepting only the lateral pair on VII, all of those on IX, and the dark brown terminal ones, IX with the three major pairs respectively 97, 110, and 68μ; tube one-half the length of head and nearly 1.9 times as long as greatest subbasal width, which is about 1.7 times the apical width, sides straight.

Measurements of female (holotype), in mm.: Length about 1.32 (fully distended, 1.65); head, length 0.174, width across eyes 0.128, least width just behind eyes 0.126, greatest width across cheeks 0.132, least width near base 0.112; prothorax, median length of pronotum 0.109, width (inclusive of coxæ) 0.214; mesothorax, width across anterior angles 0.207; metathorax, greatest width 0.207; abdomen, greatest width (at segment IV) 0.235; tube (segment X, only), length 0.087, greatest subbasal width 0.046, least apical width 0.027; terminal setæ, length 0.133.

Antennal segments:	1	2	3	4	5	6	7	8
Length (μ):	29	41	41	44	43	37	38	27
Width (μ):	31	26	25	28	25	23	20	12

Total length of antenna 0.300 mm.

Male (macropterous).—Identical with female in color and very similar to it in structure, though smaller and more slender; allotype with head 156μ long, 120μ across eyes, 117μ just behind eyes, 125μ across cheeks, and 104μ near base; sternum VIII with the glandular area forming a transverse band across middle, the width of this band about one-half the length of the segment.

North Carolina: Rocky Point (Pender County), October 20-22, 1937, J. D. H., 5 ♀♀ and 3 ♂♂, under bark on dead branches of *Pinus palustris* (holotype, allotype, and paratypes).

Florida: Orlando, November 8, 1914, Dr. C. B. Williams, 1 ♀, from grass [Williams' No. 526] (paratype).

This little species looks almost exactly like *merrilli* and is extremely closely related to it. Its size, however, is distinctly greater than that of *merrilli;* the median pair of setae on abdominal segment IX are pointed, instead of dilated, at the tip; and the metanotal apodemes are larger, less clearly defined, and not circular in dorsal aspect.

I take especial pleasure in naming it after Prof. C. S. Brimley, whose name has been associated with North Carolina entomology for many years.

Eurythrips dissimilis sp. nov.

Female (brachypterous).—Length about 1.4 mm. (fully distended, 1.79 mm.). Color light brown, somewhat overlain with gray, head yellow in front of eyes, abdomen shading to dark brown in about last three segments, tube narrowly brown at base and at apex, intermediate portion black; internal pigmentation dull ochraceous; legs pale brownish yellow, the femora and tibiæ shaded with brown, especially externally, tarsi yellow; antennæ with segment I pale brownish yellow, II somewhat darker because shaded with brown along sides, III-VIII successively darker, the yellowish color predominating in III-V, III largely yellow but shaded with gray-brown across apex and at sides in distal half, IV yellowish brown, shaded apically and at sides and with a narrow pale line across distal end of pedicel, V similarly colored but darker, VI and VII with pedicels pale, VII and VII dark gray-brown; major setæ on body brown.

Head about 1.28 times as long as greatest width, which is at middle of cheeks, the latter evenly rounded to eyes and to base, indistinctly serrate as seen from above because of short anastomosing lines which do not extend onto dorsum of head except faintly at extreme base; head slightly constricted at posterior lateral margin of eyes, at this point narrowest; vertex rounded and somewhat swollen, scarcely overhanging, its surface smooth and with the two usual pairs of setæ; postocular setæ blunt at tip, only 37μ long, 98μ apart, and arising very close to eyes; postocellar setæ minute. Eyes coarsely facetted but not moruloid and not strongly protruding, about 0.27 as long as head, their dorsal length about 51μ. Ocelli about 14μ in diameter. Antennæ normal, segments IV-VII with short pedicels, III subtriangular, IV and V subglobose; sense-cones slender, arranged as follows on inner (and outer) surfaces of segments: III 1 (1), IV 1 (2), V 1 (1 + 1), VI 1 (1 + 1), VII 1 dorsal. Mouth-cone broadly rounded at tip, extending about 106 microns beyond posterior dorsal margin of head.

Prothorax along median line of pronotum about 0.85 as long as head and (inclusive of coxæ) only 1.74 times as wide as long, without distinct median thickening, smooth excepting for a few faint striæ near posterior margin; epimeron not fused with pronotum; antero-marginal setæ minute (5 or 6μ) and pointed, the others blunt, antero-angulars 18μ, midlaterals 35μ, epimerals 44μ, postero-marginals 50μ, and coxals 27μ. Legs normal; fore tarsi with a strong tooth on inner surface at middle of first segment. Wing-pads small, about 56μ long.

Abdomen broad and heavy, but only 1.8 times as wide as prothorax across coxæ, dorsal surface almost smooth; major setæ on segments I-VI blunt, the others pointed, lateral pair on VII 84μ long, the three pairs on IX 107, 87, and 104μ, respectively; tube (segment X, only) about 0.6 as long as head, 1.49 times as long as greatest subbasal width (which is across collar), this about 2.3 times the apical width, sides tapering only slightly in basal fifth, straight and strongly tapering beyond.

Measurements of female (holotype), in mm.: Length about 1.42 (fully

distended, 1.79); head, length 0.188, width across eyes 0.133, least width just behind eyes 0.128, greatest width across cheeks 0.147, least width near base 0.136; prothorax, median length of pronotum 0.160, width (inclusive of coxæ) 0.279; mesothorax, width across anterior angles 0.231; metathorax, greatest width 0.221; wing-pads, length 0.056; abdomen, greatest width (at segment V) 0.329; tube (segment X, only), length 0.113, greatest subbasal width 0.076, least apical width 0.033; terminal setæ, length 0.083.

Antennal segments:	1	2	3	4	5	6	7	8
Length (μ):	40	47	45	45	45	45	38	29
Width (μ):	39	33	30	31	30	27	23	12

Total length of antenna 0.334 mm.

FLORIDA: Sebring, April 7, 1938, John W. H. Rehn, 1 ♀, swept from grass.

The strong tarsal tooth and non-dilated major setæ place this species as a relative of *tarsalis;* but the minute postocellar setæ will readily differentiate it, as will also the larger eyes and the much greater width of the head just behind them.

Stephanothrips carolina sp. nov.

Female (apterous).—Length about 1.2 mm. (fully distended, about 1.4 mm.). Color dark brown or blackish brown, head darkest, tube brownish yellow but shading in apical fifth to nearly black at tip; internal pigmentation of two kinds, one red and quite generally distributed in head, thorax, and abdominal segments I-VIII, the other snow-white by reflected light and forming a series of dorsal markings visible through pale areas in the integument, as follows: (1) a narrow band occupying posterior margin of pronotum and terminating in the epimera, but prolonged medially nearly to anterior margin of pronotum, (2) a median blotch involving most of the length of metanotum and of tergum I of abdomen, (3) a spot at each side of mesonotum, metanotum, and tergum I of abdomen, and (4) a spot at lateral third of abdominal terga II-VIII, these last smaller and less distinct on the more posterior segments; legs concolorous with body, except for the yellow trochanters and bases of femora, and the brown tarsi; antennæ with segment I brown, II pale yellow, III yellow but darker than II and lightly shaded with brown apically, IV dark brown; major setæ all colorless, except the nearly black terminal ones.

Head normal in form, 1.1 times as long as greatest width, which is at basal fourth, the cheeks very slightly concave at their anterior third and slightly narrowed at base; dorsal and lateral surfaces tuberculate as usual, except that the tubercles in the median region are not distinctly transverse; vertex little produced in front of eyes, with four relatively small tubercles from which arise the "crown" setæ, these last compressed and divided at tip (thus not dilated in dorsal aspect), the median pair about 33μ long and with their tips nearly or quite touching, the lateral pair about 21μ and diverging at 90°. Eyes small, consisting of three dorsal and two anterior facets. Antennæ four-segmented, III comprising (morphologically) III-V, and IV comprising VI-VIII. Mouth-cone broadly rounded at tip, extending about 78μ beyond posterior dorsal margin of head; labrum relatively short and broad, its length

about 63μ, its basal width (internal to the chitinous marginal line) about 36μ; maxillary palpi short, the second segment about 30μ.

Prothorax with median line of pronotum about 0.58 that of head and contained in trans-coxal width 2.45 times; dorsal surface tuberculated and with the usual broad fovea each side of median line; epimeral setæ 20μ long and 9μ wide at tip. Meso- and meta-thorax normal. Legs normal, their fore and hind tarsi without claw on outer surface.

Abdomen normal; tube fully 1.1 times as long as head and nearly 1.4 times as long as segment IX; dorsal sculpture distinct, forming moderately evident reticles in median portion of segments III-IX.

Measurements of female (paratype), in mm.: Length about 1.18 (fully distended, 1.39); head; length (exclusive of vertical tubercles) 0.174, greatest width (inclusive of tubercles) 0.158, least width near base 0.152; prothorax, median length of pronotum 0.101, width (inclusive of coxæ) 0.255; mesothorax, width across anterior angles 0.221; metathorax, greatest width 0.291; abdomen, greatest width (at segment II) 0.300; segment VI, median length 0.048, VII 0.054, VIII 0.052, IX (exclusive of apical spine) 0.145; tube (X, only), length 0.199, greatest subbasal width 0.029, greatest apical width 0.035; terminal setæ, length 0.424.

Antennal segments:	1	2	3	4
Length (μ):	24	40	78	64
Width (μ):	26	32	33	21

Total length of antenna 0.206 mm.

Male (apterous).—Smaller, but otherwise virtually identical with female.

Measurements of male (allotype), in mm.: Length about 0.90 (partially distended, 0.97); head, length 0.139, greatest width 0.133; inner pair of vertical setæ, length 0.023, outer 0.015; mouth-cone, extent beyond posterior dorsal margin of head 0.058; prothorax, median length of pronotum 0.085, width (inclusive of coxæ) 0.196; epimeral seta, length 0.013; mesothorax, width across anterior angles 0.171; metathorax, greatest width 0.204; abdomen, greatest width (at segment II) 0.211; segment IX, median length 0.109; tube, length 0.143, greatest subbasal width 0.024, greatest apical width 0.030; terminal setæ, length 0.378.

Antennal segments:	1	2	3	4
Length (μ):	--	40	68	62
Width (μ):	--	27	30	20

North Carolina: Rocky Point (Pender Co.), October 21, 1937, Dr. R. W. Leiby and J. D. H., 24 ♀♀ and 1 ♂, from dead branches of *Liquidambar* and other trees.

Allied to *S. fusiantennatus* and *S. corticinus*, but readily separable by the shorter head, shorter ninth abdominal segment, shorter and broader labrum, shorter maxillary palpi, and the heavier tergal sculpture of the abdomen.

Dept. of Entomology,
Cornell University,
Ithaca, N. Y.

Descriptions of New Ants from the Western United States

A. C. Cole, Jr.

Formica oregonensis sp. nov.

Holotype, worker. (Cole collection No. 440).

Total length, 5.9 mm.

Body slender. Head, excluding mandibles, broader than long, narrower in front than behind, with rather straight sides and feebly convex posterior border; corners well rounded. Mandibles large, convex, with eight blunt teeth; apical tooth longest, other teeth alternately long and short. Clypeus convex, carinate, its anterior border distinctly and broadly excised. Frontal area distinct, triangular, its base and height subequal. Frontal groove faint and extending only about two-thirds the distance from the frontal area to the median ocellus. Frontal carinae not divergent behind. Antennae rather slender; scapes curved, gradually thickened toward their tips. Eyes rather large.

Thorax long and slender; pro- and mesonotum moderately convex; promesonotal impression very faint in profile; mesoepinotal suture rather shallow and very broad; epinotum broadly angular in profile, with subequal base and declivity. Petiolar scale broad, its base thick, the summit thin, convex, entire, with rather flat anterior and slightly convex posterior surface. Legs long and slender. Gaster stout.

Body shining and very finely shagreened. Mandibles finely rugose; clypeus delicately striatopunctate; space between frontal carinae with very fine striae diverging posteriorly at the posterior extremity of the frontal groove. Frontal area smooth and shining. Epinotum very finely reticulate-rugose, giving it a less shining appearance than the other parts. Gaster very smooth and shining.

Hairs yellow, long, slender; blunt on thorax and gaster, pointed on head; rather sparse; most numerous on head and dorsum of pro- and mesonotum; longest on head; sparse, short and closely appressed on antennal funiculi, more abundant on terminal segments; absent from scapes and lateral surfaces of head and thorax; long, curved and rather numerous on mandibles; very long and sparse on clypeus; very sparse on gula and dorsum of epinotum. Anterior femora with a row of sparse, long, slender hairs bordering the flexor surfaces. Hairs long and erect on ventral surface of coxae. Posterior surface of petiolar scale with a single row of hairs just below the superior border. Hairs short and sparse on dorsum of gaster, long and numerous on venter and around anus. Pubescence very short and sparse.

Color carob brown. Legs (except coxae), mandibles (except border and

teeth), antennae, clypeus and genae lighter. Tips of antennal funiculi infuscated. Gaster deep black throughout. Dorsum of pronotum with an infuscated area.

The holotype was selected from a series of sixteen workers collected by the author near Pendleton, Oregon, July 11, 1931. The ants were attending aphids on an herb in an alpine meadow above the timberline. The nest was not found. The holotype and a series of paratypes are in the author's collection. Paratypes are to be deposited in the U. S. National Museum.

Variation in paratype material.—The color is rather constant throughout the series. In a few specimens the legs, especially the tibiae and tarsi, are somewhat paler. The length varies from 4.5 to 6.5 mm. In the smaller workers the head is as long as broad, the clypeal carina is somewhat more pronounced and the clypeal border is more faintly excised. Some of the larger workers have deeper and hence more prominent impressions in the anterior clypeal border than do the others. The epinotum of a few of the specimens is without hairs, while most specimens bear only a single dorsal pair. Each of two specimens has a group of about ten hairs on the dorsum of the epinotum. One specimen is somewhat more uniformly hairy than are the others and the hairs on the thorax are less blunt. In two specimens the petiolar scale is as light colored as the legs and antennae. All specimens show at least a light infuscation of the pronotal dorsum. In two specimens the sides of the pronotum and the entire mesonotum are of a much lighter shade than the epinotum and coxae.

Affinities.—The notched clypeus of *F. oregonensis* places this species definitely in the Sanguinea Group of the subgenus *Formica.* The specimens key down to *F. manni Wheeler,* to which they are undoubtedly rather closely related, but they differ from *manni* in the following respects: (1) Head of larger workers, exclusive of mandibles, broader than long; (2) antennal scapes incrassated toward their tips; (3) superior border of petiolar scale consistently entire; (4) hairs yellow, sparse on the gula; (5) very dark reddish brown in color; and (6) average larger in size.

F. oregonensis is similar to *F. perpilosa* Wheeler in breadth of the head, the incrassated tips of the antennal scapes and the single row of hairs on the flexor surfaces of the femora. It differs from *perpilosa,* however, especially in the subparallel frontal carinae of the head, the less convex mesonotum, the broader and shallower mesoepinotal constriction, the flattened anterior surface of the petiolar scale, the sparse pilosity, the very sparse pubescence and the much deeper color.

Formica pallide-fulva subsp. **delicata** nov.

Holotype, worker. (Cole collection No. 588).

Total length, 5.2 mm.

Body rather slender. Head, excluding the mandibles, longer than broad, narrower in front than behind, with slightly convex posterior and lateral borders and very rounded posterior corners. Eyes large; ocelli distinct. Man-

dibles large, broad, curved, 8-toothed; apical tooth long, all teeth rather sharp and pronounced. Clypeus strongly carinate its entire length except near its junction with the frontal area; with entire, rounded, projecting anterior border. Frontal area distinct, well depressed. Frontal carinae subparallel, not diverging posteriorly. Frontal groove wanting. Antennae long and slender; the scapes extending about two-thirds their length beyond posterior margin of the compound eyes, thickened from base to apex; basal joints of funiculi more slender than penultimate joints, subcylindrical. Maxillary palpi very long.

Thorax narrow. Pronotum evenly convex in profile; promesonotal suture well marked. Anterior margin of mesonotum higher than the pronotum; posterior mesonotal declivity feebly convex, long, meeting the epinotum at the deep and rather broad mesoepinotal suture. Epinotum very convex, its dorsal surface and declivity subequal and their junction broadly curved, the declivity flattened and rather strongly oblique in profile. Scale of petiole rather narrow, thick, cuneate in profile, with very convex and somewhat flattened posterior surface; its border rather sharp, broadly rounded when seen from behind, with a distinct and rather broad notch; lateral borders slightly rounded. Legs long and rather slender. Gaster large.

Entire body subopaque and very finely shagreened; gaster more shining. Mandibles rather finely and longitudinally striatopunctate. Clypeus, mesothoracic sternites and epinotum very faintly striate.

Hairs yellowish and sparse; long, slender, sharp and erect on frons, vertex, clypeus and mandibles; absent from eyes, gula, genae, antennal scapes and pronotum; short and erect on mesonotum; almost absent from epinotum and petiole; more abundant on gaster, where they are short and suberect and arranged in three or four rows on each segment, and on ventral surface of coxae where they are long, erect and slender. Pubescence whitish, short and sparse; abundant only on middle and hind coxae and on anterior surface of petiolar scale; extremely sparse on head, thorax and gaster.

Color Argus brown; clypeus and mandibles a little darker; anterior border of mandibles and mandibular teeth dark brownish-black; gaster and tips of antennal funiculi lightly infuscated.

Paratype, nest queen. (Cole collection No. 588).

Total length, 9.1 mm.

Head longer than broad but more rectangular than that of the worker; lateral margins almost straight. Frontal groove distinct the entire distance from frontal area to median ocellus. Antennal scapes extending a little more than half their length beyond the posterior margins of the compound eyes; funicular joints thicker than those of the worker. In other respects the head is like that of the holotype.

Thorax about twice as wide as the head, subovoid when seen from above, its widest point at the attachment of the remnants of the fore wings. Promesonotal suture well marked. Scutum as broad as long; in profile broadly convex anteriorly, almost flat apically. Scutellum feebly convex in profile, a

little higher than the scutum; lateral projections narrow, long and blunt at the apex. Metanotum rather narrow, much lower than the scutellum, convex medianly but depressed at the wing insertions; angle between scutellum and metanotum sharp. Epinotum a little lower than metanotum, higher than long; in profile its dorsal surface short and sloping, its juncture with the declivity rounded, the declivity much longer and more oblique than the dorsal surface. Petiolar scale with the superior border sharper than that of the worker and more compressed at the corners; posterior surface much more flattened. Gaster oval, rather broad. Legs shorter than those of the worker and the tibiae stouter.

More shining than the holotype. Scutum, scutellum and gaster very smooth and shining, the head less so; epinotum and petiolar scale opaque. Hairs golden, longer and more slender than those of the worker; absent from superior border of petiolar scale, almost absent from epinotum, sparse elsewhere; gula with two long hairs. Pubescence long, white and abundant on anterior declivity of pronotum, on epinotum, coxae and anterior face of petiolar scale; extremely sparse elsewhere. Mandibles striate and with a few rugae.

Pronotum, scutum, legs and antennae Argus brown; head, scutellum and thoracic sutures darker; scale of petiole lighter; epinotum grayish because of the dense pubescence. Gaster chestnut brown, anal region and borders of segments lighter.

The holotype and the paratype queen were selected from a series of fourteen workers and one nest queen collected by the author at Ten Sleep, Wyoming, September 21, 1931, from a mound of twigs. The mound was beside a clump of sagebrush in a rocky area.

Affinities.—The specimens, both workers and queen, show a definite relationship to the subgenus Neoformica. The workers are structurally close to those of *F. pallide-fulva* subsp. *nitidiventris* Emery, but differ in the longer narrower head and in the possession of very sparse hairs on the superior border of the petiolar scale. The female differs from that of *nitidiventris* in that her head is more narrow and decidedly longer than broad, exclusive of the mandibles. She is larger than the female *nitidiventris*, and more closely approximates the length of *schaufussi*. There are also two long hairs on the gula which are absent from the female of *nitidiventris*.

Variation in paratype material.—In the paratype series of workers the total length of the body varies from 4.8 to 6.2 mm. There is little variation in other respects. The gaster of two specimens is a little darker in color than are the gasters of other members of the series; and in two specimens the hairs are absent from the petiolar scale.

Myrmecocystus melliger subsp. *semirufus* Emery

Replete. (Cole collection No. 783).

Total length, 5.8-6.1 mm.

Color paler than that of the regular worker and more reddish throughout;

head and thorax chestnut. Gaster distended in diameter two to three times that of the worker. In all other respects like the ordinary worker.

These repletes of *M. semirufus* were collected by the author from chambers beneath a small crater mound of sand, about six inches in diameter, in a very sandy area with scant vegetation, 10 miles south of Cameron, Arizona, May 15, 1932. The author has collected many specimens of *semirufus* from nests at various localities in California, Arizona, and New Mexico, in none of which except the locality designated were repletes found. The specimens were taken from chambers fully three feet beneath the nest entrance.

In so far as I have been able to ascertain, this is the first record of a replete in nests of *semirufus* or its varieties, and shows that we are likely to discover the replete condition among some Myrmecocysti now supposed to be without this form.

Pheidole pilifera subsp. *artemisia* Cole.

Specimens were collected by the author from a nest of this subspecies at the type locality (Provo, Utah), May 13, 1932. Among them was a single nest queen which I describe as follows:

Topotype, nest queen. (Cole collection No. 751a).

Total length, 5.0 mm.

Head, excluding mandibles, distinctly broader than long, a little broader behind than in front, with very faintly and broadly excised posterior margin; vertical groove pronounced and extending to clypeus; clypeus convex, especially at apex, without a median carina, anterior margin faintly but definitely excised. Mandibles convex, with two apical teeth, one small basal tooth and a few minute and irregular intermediate teeth. Frontal area subtriangular, moderately impressed, with a median carinula. Ocelli large. Tips of antennal scapes reaching more than half the distance between the eye and the posterior corner of the head. Thorax robust, between wing insertions as broad as the head. Mesonotum and scutellum flattened. Epinotum like that of the soldier; spines robust, rather sharp, more than twice as far apart at base as long, directed upward, outward and backward. Petiole with acute tooth-like anterior corners and slightly concave sides; its apex rather blunt and broadly excised, its posterior superior surface concave. Postpetiole less than twice as broad as the petiolar node, its lateral prolongations blunt and concave posteriorly. Gaster elliptical, longer and broader than the thorax.

Mandibles and clypeus shining, very finely punctate and with a few striae near their bases. Frontal area subopaque, more coarsely punctate and with a single faint striation on each side of the median carinula. Head coarsely and longitudinally rugose, with finely punctate interrugal spaces. Mesonotum and scutellum finely and densely punctate, the former with rather coarse longitudinal striae on its posterior half. Epinotum subopaque, punctate-rugulose on the sides; infraspinal facet with fine, transverse rugae and punctures. Petiole

and postpetiole subopaque, finely and densely punctate. Gaster moderately shining, very finely shagreened.

Hairs yellow, abundant, suberect, more appressed on gaster, legs and antennae; pointed and delicate; sparse on anterior surface of petiole and mesothoracic sternites and episternites. Pubescence absent.

Light seal brown; mandibles, clypeus, ocelli, anterior third of head, legs and antennae lighter.

All descriptions in this paper are based upon dried alcoholic specimens. Colors of all major body regions are those listed and illustrated by Robert Ridgway in, "Color Standards and Color Nomenclature." Comparisons of the ants with the color plates were made without magnification in the light of a 100-watt Mazda bulb provided with a metal reflector. Colors were matched with the bulb one foot directly above the specimens which were placed on the color plates. When the correct shade had been obtained there was a decided blending of the color of the specimen with that of the plate. Comparisons were made by two other persons, and in each case their determinations were the same as those of the author. Colors of the smaller structures, such as ocelli, mandibles, palpi and antennae, are those of the writer's conception and were determined under a magnification of 30 diameters. Measurements of size are to the closest tenth of a millimeter.

The writer is indebted to Dr. W. S. Creighton, College of the City of New York, for his kindness in comparing specimens of *F. oregonensis* sp. nov. and *F. pallide-fulva* subsp. *delicata* nov. with related forms in the American Museum of Natural History.

Dept. of Entomology,
University of Tennessee,
Knoxville, Tenn.

Contributions to Texan Herpetology VII.

THE SALAMANDERS

Charles E. Burt

The data presented in this series were gathered during the years 1930-1936. The collections, comprising representatives of seventeen species, are for most part in the U. S. National Museum. Moreover all of the specimens from Texas in that institution have been studied critically.

Key to the Salamanders of Texas

1. External eyes present; body usually more or less pigmented; surface salamanders_2
1. Eyes not visible externally; body white; legs long and slender, weak; perennibranchiate, gills conspicuous with filaments simple, long and slender; living in subterranean waters. Texan blind cave salamander.
Typhlomolge rathbuni Stejneger
2. Hind limbs normally developed, with four or five toes _____5
2. Hind limbs poorly developed or absent, toes three or fewer when present; adults large, gray or blackish in color. _____3
3. No hind limbs; front limbs vestigial, with four digits. _____4
3. Four limbs present, all vestigial, each with fewer than four digits. Southern Congo eel. _____*Amphiuma tridactylum* Cuvier.
4. Costal grooves usually more than 35; adult large, frequently over 400 mm. from snout to cloaca. Giant mud eel. _____*Siren lacertina* Linné
4. Costal grooves usually 35 or less; adult usually 200 to 300 mm. Dwarf mud eel. _____*Siren intermedia* Le Conte
5. Five toes on hind feet. _____8
5. Four toes on hind feet. _____6
6. External gills not present in adults; body not over 50 mm. long. _____7
6. Perrenibranchiate; adults over 100 mm. long. Common mudpuppy.
Necturus maculosus maculosus (Rafinesque)
7. Tail constricted at base; belly white, with black spots; tongue attached in front; 14 costal grooves. Four-toed salamander.
Hemidactylium scutatum (Schlegel)
7. Tail tapering evenly from base; belly suffused with yellow in life, not with prominent black spots; tongue free in front, mushroom shaped; over 14 costal grooves. Dwarf salamander.
Eurycea quadridigitata quadridigitata (Holbrook)
8. Costal grooves visible on sides (a series of vertical furrows between insertions of front and hind limbs); other characters variable. _____10
8. No costal grooves visible on sides; tail strongly compressed from sides; numerous small black dots or reticulations usually present on body, including undersurface; newts. _____9
9. A longitudinal series of conspicuous ocelli (dark margined round spots with light centers) present on each side, centers usually colored red or pink in life. Crimson spotted newt. _____*Triturus viridescens viridescens* Rafinesque
9. No series of ocelli. Gulf newt. _____*Triturus viridescens meridionalis* (Cope)

10. No light line running obliquely from eye to angle of jaw; other characters variable. ---------- 11

10. A light line running obliquely from eye to angle of jaw; costal grooves usually 14; body usually not over 60 mm. long. Western dusky salamander. *Desmognathus fuscus brimleyorum* Stejneger

11. Belly usually dark often blue black; some species with conspicuous white or yellow spots, or bars on body. ---------- 13

11. Belly lighter, often suffused with yellow in life; never with large spots or bars, back and sides with dark and light mottlings. ---------- 12

12. Costal grooves usually 13 or 14; sides of body deeply pigmented; some mottling on lower sides and often a fine slaty reticulation on belly. Dark sided salamander. ---------- *Eurycea melanopleura* (Cope)

12. Costal grooves 15 to 17; sides of body somewhat lighter; no pigment on lower sides and belly; apparently perribranchiate, known adults with small gills. Neotenic salamander. ---------- *Eurycea neotenes* Bishop and Wright

13. Tail not rounded, more or less compressed from sides, usually having a dorsal keel or ridge for part of its length; light markings large in several forms; ground color variable. ---------- 14

13. Tail definitely rounded but sometimes slightly compressed very close to tip only, no dorsal keel; never with large light spots, but usually with small white stipplings on blue-black ground color, especially on the sides. Spotted slimy salamander. ---------- *Plethodon glutinosus* (Greene)

14. Large light spots *or* bars on body. ---------- 15

14. Body blue black or grayish without large light spots or bars. Texas salamander. *Ambystoma texanum* (Matthes)

15. Body with yellow, orange or reddish spots in life; these round, ovoid *or* in transverse bars that are largely alternated or broken at the vertebral line. ---- 16

15. Body and tail crossed by conspicuous transverse white or bluish white bars that run from side to side, these rarely broken at the vertebral line. Marbled salamander. ---------- *Ambystoma opacum* (Gravenhorst)

16. Spots round or nearly so, confined to sides; two conspicuous folds between eye and insertion of forelimb. Spotted salamander. *Amblystoma maculatum* (Shaw)

16. Spots frequently elongated into alternating transverse bars that may approach vertebral line; one conspicuous fold between eye and insertion of forelimb. Tiger salamander. ---------- *Amblystoma tigrinum* (Green)

List of Species

Necturus maculosus maculosus (Rafinesque)

Mudpuppies have been taken at many localities in the Mississippi River drainage basin, including Oklahoma and Louisiana, and they are likely to occur in the waters of northeastern Texas. But when Viosca (1937) revised the genus he listed no Texas records.

Amphiuma tridactylum Cuvier

The Congo eel was reported from Bowie County by Strecker and Williams (1928). It occurs in extreme northeastern Texas.

Triturus viridencens viridescens Rafinesque

The crimson spotted newt occurs at least in east-central and northern Texas. When the animal is preserved its red spots on the sides fade to

white. A small specimen with red ocelli was taken on May 9, 1931, in damp rotted wood above the margin of a small pond 6 miles east of Palestine, Anderson County. The U.S.N.M. has specimens of this newt from Falls and Victoria counties, and Strecker and Williams (1928) found it in Bowie County.

Triturus viridescens meridionalis (Cope)

The newts of the *viridescens* complex form a well delineated group, but the status of the various subspecies is not clear. It appears that there are two subspecies in Texas, one *(viridescens)* with red-centered ocelli on the sides and one *(meridionalis)* without these ocelli. The ranges of the two forms have not been ascertained, but along the coastal plain of southeastern and central Texas *meridionalis* is most common, while *viridescens* occurs in the northeast. Dunn (1918) listed the southern form as occurring as far north as Dallas. Intergradation is evident in Victoria County, where gradual and complete transition can be demonstrated in a large series of specimens (U.S.N.M.).

Triturus viridescens louisianae Wolterstorff (1914), originally described from New Orleans, Louisiana, has no ocelli on the sides, and since it is in the coastal range of *meridionalis* it may be the same species. There seem to be no adequate grounds for recognizing *louisianae* as a Texan subspecies. Earlier writers recorded *meridionalis* from Bexar, Dallas, Duval, Falls, Harris, Liberty, McLennan and Victoria counties. New records are: Brazoria County at Velasco (William Lloyd, March 1892); and Marion County at Carter Lake east of Jefferson (Ottys Sanders, April 1, 1934).

Ambystoma maculatum (Shaw)

The first definite record of the occurrence of the spotted salamander in Texas was given by Strecker and Williams (1928) who on March 6 secured it from the Sulphur River bottoms of Bowie County. On June 17, 1934, I secured a second specimen in the moist sawdust under a pile of boards near a small streamlet four miles south of Mt. Enterprise, Rusk County.

Ambystoma opacum (Gravenhorst)

The U.S.N.M. has marbled salamanders from San Jacinto County (G. H. Ragsdale), as well as a specimen that I collected in Rusk County in association with the *maculatum* mentioned above. The literature records *opacum* also in Bowie, Lamar, Liberty, McLennan, and Wichita counties.

Ambystoma texanum (Matthes)

This is apparently the commonest and most characteristic salamander of Texas. Many of the former records have been published under the synonym *microstomum*. The adults are usually found in damp situations in piles of trash or under stones, pieces of tin, old logs, or boards near bodies of water. The young, however, are strictly aquatic, occurring frequently in the smaller streams and ponds where a moderate growth of pond weeds and algae affords

protection, freshens the water, and provides food for the small organisms on which they live.

Few data were secured pertaining to the life history. On March 5 an adult was active at night in the vicinity of a small prairie pond near Dallas. On March 29 23 larvae, none of which measured over 35 mm. in length, were taken in a small stream near Fort Worth. On April 17, 23 larvae were secured in a streamlet near Decatur, some of which had attained a length of over 40 mm. Comparative study of living material has shown that the youngest specimens exhibit a series of prominent vertical light bars or spots in addition to a distinctive longitudinal light stripe on each side of the body and tail. At first sight such individuals may be taken for similar colored minnows. As development progresses these markings are gradually diffused and lost, the vertical bars being the first to become indistinct. Later, as even the longitudinal stripes grow duller, a uniform olivaceous coloration is approached and the larval *texanum* then becomes more difficult to distinguish from specimens of *tigrinum* of corresponding size.

The literature records *texanum* from Bexar, Bowie, Brazos, Burnet, El Paso, Falls, Harris, Henderson, Lamar, Liberty, McLennan, Refugio, Robertson, Tarrant, Travis, Uvalde, Victoria and Wilson counties. New reports follow.

County	Locality	Date	Collector
Comal	3 mi. s.w. New Braunfels	April , 1931	C. E. Burt
Cooke			G. H. Ragsdale
Dallas	4 mi. s. Dallas	March 5, 1931	C. E. Burt
Ellis	Waxahachie	March 26, 1931	C. E. Burt
Parker	12 mi. e. Weatherford	April 18, 1931	C. E. Burt
Tarrant	4 mi. w. Fort Worth	March 29, 1931	C. E. Burt
Wise	6 mi. s. e. Decatur	April 17, 1931	C. E. Burt

Ambystoma tigrinum (Green)

On April 4, 1931, 45 metamorphosing young of the tiger salamander were secured near Encino. The smallest individual was 50 mm. long. Some of the larvae were uniformly olivaceous in dorsal ground color; others were darker and displayed a series of more or less distinct yellow bars on the sides. The habitat was a pond divided by a fence. It was found that salamanders were not present on the side frequented by cattle, where dippings produced a distinctly bovine odor. The literature lists specimens from Armstrong, Bexar, Burnet, El Paso, Garza, Henderson, Lampasas, Pecos, Tarrant and Ward counties. New records are given below.

County	Locality	Date	Collector
Brooks	2 mi. s. Encino	April 4, 1931	C. E. Burt
Culberson	Guadalupe Mts.	August 24, 1901	V. Bailey
Potter	Amarillo	June 3, 1899	V. Bailey
Terry	Brownfield	January 15, 1931	O. Sanders

Hemidactylium scutatum (Schlegel)

In his monographic study of the Plethodontidae Dunn (1926) included Texas in the range of the four-toed salamander. There are no definite records of locality but three specimens in the collection of the Museum of Comparative Zoology (No. 206) are labelled as having come from the State.

Plethodon glutinosus (Green)

Previous workers have reported the spotted slimy salamander from Bexar, Comal, Hays, Liberty and McLennan counties. Bell County is added because of my discovery on March 6, 1931, of seven individuals in a deep ravine 3 miles south of Belton. These specimens were removed from under stones and dead leaves kept damp by seepage from springs. When disturbed, the salamanders attempted to escape by moving toward crevices in the rocks, rather than toward shallow pools of water.

Typhlomolge rathbuni Stejneger

The 39 individuals of this form in the U.S.N.M. are all albinistic and excellently present the characters described for this species. These peculiar salamanders are blind and live in underground waters. The National Museum series was collected by members of the U. S. Fish Commission from the underground channel of an artesian well at San Marcos, Hays County. The original description (1892) is a fine taxonomic treatise, and interesting observations on the habits of the species were added by Uhlenhuth (1921), who mentioned specimens from new localities in Hays County; from Burnet Cave, Kendall County; and from Ozona, Crockett County.

Eurycea melanopleura (Cope)

Dunn (1926) included Texas in the range of the dark-sided salamander. There are no definite locality records but the Museum of Comparative Zoology has a specimen (No. 244) labelled from Texas.

Eurycea neotenes Bishop and Wright

This new neotenic salamander was described recently (1937) from Culebra Creek 5 miles north of Helotes, Bexar County. Its closest relative appears to be *E. bislineata.*

Eurycea quadridigitata quadridigitata (Holbrook)

Dwarf salamanders are found beneath debris near the small streams and ponds in the woods of East Texas where they are often very agile during warm summer days. The species has been reported previously from Anderson, Bowie, Cass and Marion counties. New records are given below.

County	Location	Date	Collector
Hardin	5 mi. n.w. Kountze	July 6, 1934	C. E. Burt
Sabine	5 mi. s.w. Pendleton Ferry	June 17, 1934	C. R. Rogers
Tyler	Hillister	July 6, 1934	W. L. Hoyle

Desmognathus fuscus brimleyorum Stejneger

Dunn (1926) included Texas in the range of this dusky salamander on the basis of a specimen from Waco, McLennan County, in the collection of the Field Museum of Natural History.

Siren intermedia LeConte

The characters of the dwarf mud eel (as used in the present key) were diagnosed by Noble and Marshall (1932), who found Texas specimens more or less intermediate with the following species. They definitely identified some U.S.N.M. specimens from Maverick and Victoria counties as *intermedia*, but listed *lacertina* from the same places. I am unable to make a critical study at present, so the available records are summarized below under *lacertina*, the name by which they were first reported.

Siren lacertina Linné

The ground color of the giant mud eel varies from black in the young to light gray in older specimens. Two specimens from Rockport have the sides distinctively variegated with patches and spots of pinkish color. The literature records specimens from Bexar, Bowie, Calhoun, Dallas, Duval, Harris, Henderson, Kaufman, Leon, Liberty, Maverick, McLennan, Refugio, Smith, Tarrant and Victoria counties. New reports follow.

County	Location	Date	Collector
Aransas	Rockport		H. P. Attwater
Cameron	Ft. Brown near Brownsville	March 1, 1915	R. D. Camp
Jackson	Edna		G. E. Lewis

REFERENCES

Bishop S. C. and Margaret R. Wright. 1937—A new neotenic salamander from Texas. Proc. Biol. Soc. Washington **50**:141-144.

Cope, Edward D. 1880—On the zoological position of Texas. Bull. U. S. Nat. Mus. **20**:1-51.

———1889—The Batrachia of North America. *Ibid.* **34**:1-525, text figs. 1-115, pls. 1-83.

Dunn, Emmett R. 1918—The collection of Amphibia Caudata of the Museum of Comparative Zoology. Bull. Mus. Comp. Zool. **62**:445-471.

———1926—The salamanders of the Family Plethodontidae. Smith Coll. Fiftieth Anniv. Publ. **5**:1-441, text figs. 1-86.

Noble, G. K. and B. C. Marshall. 1932—The validity of *Siren intermedia* LeConte with observations on its life history. Amer. Mus. Novitates **532**:1-17.

Pope, Philip H. 1919—Some notes on the amphibians of Houston, Texas. Copeia **76**:93-98.

Stejneger, Leonhard. 1892—Preliminary description of a new genus and species of blind cave salamander from North America. Proc. U. S. Nat. Mus. **15**:115-117.

STONE, WITMER. 1903—A collection of reptiles and batrachians from Arkansas, Indian Territory, and Western Texas. Proc. Acad. Nat. Sci. Phila. **1902**:538-542.

STRECKER, JOHN KERN. 1902—Reptiles and batrachians of MecLennan County, Texas. Trans. Texas Acad. Sci. for 1901, **4**(2):95-101.

———1908a—The reptiles and batrachians of Victoria and Refugio Counties, Texas. Proc. Biol. Soc. Wash. **21**:47-52.

———1908b—A preliminary annotated list of the batrachians of Texas. *Ibid.* **21**:53-62.

———1909—Contributions to Texan herpetology. Baylor Univ. Bull. **12**(1):1-20.

———1910—Notes on the fauna of Northwestern Texas. *Ibid.* **13**(4-5):1-31, text figs. 1-2, pl. 1.

———1915—Reptiles and amphibians of Texas. *Ibid.* **18**(4):1-82.

———1922—An annotated catalogue of the amphibians and reptiles of Bexar County, Texas. Bull. Sci. Soc. San Antonio **4**:1-31.

———1926a—Notes on the herpetoloogy of the East Texas Timber Belt. I. Liberty County. Contr. Baylor Univ. Mus. **3**:1-3.

———1926b—Same. II. Henderson County. *Ibid.* **7**:3-7.

———1927—Herpetological records from the vicinity of San Marcos, Texas, with distributional data on the amphibians and reptiles of the Edwards Plateau Region and Central Texas. *Ibid.* **12**:1-16.

———1928—Common English and Folk names for Texas amphibians and reptiles. *Ibid.* **16**:3-21.

———1929—A preliminary list of the amphibians and reptiles of Tarrant County, Texas. *Ibid.* **19**:10-15.

———1930—A catalogue of the amphibians and reptiles of Travis County, Texas. *Ibid.* **23**:1-16.

———1935—Notes on the zoology of Texas. Baylor Univ. Bull. **38**(3):1-69.

———AND WALTER J. WILLIAMS. 1928—Field notes on the herpetology of Bowie County, Texas. Contr. Baylor Univ. Mus. **17**:3-19.

UHLENHUTH, EDUARD. 1921—Observations on the distribution and habits of the blind cave salamander, *Typhlomolge rathbuni*. Biol. Bull. **40**:73-104.

VIOSCA, PERCY. 1937—A tentative revision of the genus *Necturus* with descriptions of three new species from the Southern Gulf Drainage Area. Copeia **2**:120-138.

WOLTERSTORFF, W. 1914—Ueber *Diemyctylus viridescens* Raf. subsp. *louisianensis* n. subsp. Abhandl. u. Ber. Mus. Naturwiss. Ver. Magdeburg **2**(4):1-10, pl. 1.

A Systematic Account of the Alligator Lizards (Gerrhonotus) in the Western United States and Lower California*

Henry S. Fitch

CONTENTS

Introduction ---- 381
Characters of the genus Gerrhonotus ---- 382
Characters used in distinguishing species and subspecies ---- 385
Comparison of Gerrhonotus multi-carinatus and Gerrhonotus coeruleus ---- 387
Accounts of species and subspecies.
Gerrhonotus multi-carinatus scincicauda ---- 389
Gerrhonotus multi-carinatus multi-carinatus ---- 390
Gerrhonotus multi-carinatus webbii ---- 395
Gerrhonotus multi-carinatus nanus ---- 397
Gerrhonotus cedrosensis ---- 400
Gerrhonotus paucicarinatus ---- 401
Gerrhonotus kingii ---- 402
Gerrhonotus coeruleus principis ---- 404
Gerrhonotus coeruleus shastensis ---- 409
Gerrhonotus coeruleus coeruleus ---- 413
Gerrhonotus coeruleus palmeri ---- 418
Summary and conclusions ---- 420
References ---- 423

Introduction

Systematic study of the saurian genus *Gerrhonotus* was undertaken because it seemed probable that the abundant new material at hand would serve to clarify relationships within the group. The taxonomic changes resulting from this study already have been set forth (Fitch, 1934 *a*, 1934 *b*). The purpose of this report is to explain fully these changes and to consider in detail the relationships of all the forms that have been studied by me. The species dealt with are the northwestern representatives of the genus; four occur in the Pacific Coast region of North American, from British Columbia to Lower California, inclusive, and one in the southern Rocky Mountains region of Arizona, New Mexico, and adjoining parts of northern Mexico. I have not investigated the relationships of these forms to more southern representatives of the genus.

The material used included that in the collections of the Museum of Vertebrate Zoology, California Academy of Sciences, Leland Stanford Jr. University Natural History Museum, San Diego Society of Natural History, and Laurence M. Klauber.

* Contribution from the University of California Museum of Vertebrate Zoology.

This paper was written in 1933 as a study in natural history and systematics combined, and was based on nearly 500 specimens of *Gerrhonotus multicarinatus*, more than 400 of *G. coeruleus*, 22 of *G. kingii*, 13 of *G. paucicarinatus*, and 3 of *G. cedrosensis*. Later, the natural history data were published separately (Fitch, 1935), and the remaining material was revised somewhat and is here presented. I have examined about 160 specimens acquired by the Museum of Vertebrate Zoology since the completion of the original manuscript, and distribution maps have been brought up to date accordingly; but with a few exceptions these new specimens have not been included in the statistical summaries of scale counts.

This opportunity is taken to express thanks and appreciation to Professor Joseph Grinnell under whose guidance this paper has been prepared, for frequent stimulating counsel and suggestion. I am deeply indebted also to Dr. Jean M. Linsdale for suggestions made during the course of my work, for his criticism of the manuscript and for information regarding specimens in certain eastern museums. Thanks are due for courtesies extended in use of the collections under their care, to Mr. Joseph R. Slevin of the California Academy of Sciences, Mr. Laurence M. Klauber of San Diego, and Dr. George S. Myers of Stanford University; for criticism and suggestion, to Professors Charles L. Camp and E. Raymond Hall; and for information concerning the type specimen of *Gerrhonotus wiegmanni*, to Mr. H. W. Parker, in charge, Reptile Section, British Museum of Natural History. Assistance rendered by the WPA is acknowledged.

Characters of the Genus Gerrhonotus

In *Gerrhonotus* as in other members of the family Anguidae the tongue has a thick posterior part and a thin flattened and extensible anterior part, the teeth are pleurodont, bony dermal plates underlying the scales are present, while abdominal ribs and femoral and preanal pores are absent. Other characters of the genus are possession of a single frontal bone, an azygous prefrontal plate, palatine teeth, bifurcate hemipenes have flounces continuing to the tip without spines, and a lateral fold of skin on the body with granular scales but devoid of bony plates.

These lizards have long pointed heads, elongate bodies, and long cylindrical tails which when unbroken are from 1½ to more than 2½ times the head and body length. The limbs are pentadactyl but are small and weak. The scales are large, overlapping, and shingle-like, and are arranged in regular transverse and longitudinal rows. Those of the ventral surface do not correspond with the dorsal series and are separated from them by an area of fine granular scales, which extends from the angle of the jaw along each side to the anal region. On each side of the body beneath the insertions of forelimbs are lateral portions of transverse scale rows which are crowded out in the mid-ventral region by enlargement there of the scales of more anterior or posterior rows. Thus in counting the transverse rows one would obtain a higher number by recording those along the side of the body than in counting along the mid-line. In this study the latter count only was employed. The limbs are covered with small scales which, on the dorsal surfaces, are arranged in rows similar to, and smaller than, those of the body, but which become granular on the ventral and posterior sides. The tail has regular whorls of scales, two for each vertebral segment. On its ventral surface the body is flat

and the scales are smooth with a polished appearance. The scales of the dorsal surface are usually keeled to a greater or lesser degree. The head is covered with large flattened plates which are variable in number and proportions geographically and individually. On each side these plates typically consist of ten or eleven supralabials, one nasal, two pairs of postnasals, a loreal, three infraoculars, five supraciliaries, an outer row of three and an inner row of five supraoculars, several small postoculars, two parietals, an occipital, and several rows of temporals. Medially there are one rostral, one azygous prefrontal, one frontoparietal, one interparietal, and one or several interoccipitals. The lower jaw has a median mental plate and, on each side, three rows of infralabials of which those in the inner row are largest, and those in the outer row are smallest. Bony plates make the skin stiff and rigid, but this rigidity is compensated for by the flexible lateral fold. The fold usually is protected by overlapping ventral plates. It allows the body to expand when the lizard inflates itself with air or is distended by eggs or food.

The eyelids are paved externally with flattened granular scales. The eye is large and the iris may be either heavily clouded with dark pigment, or of a light yellow color. The pupil is roughly circular but has an angle projecting above and one below. These angles, apparently, allow for dilation. The eye in *Gerrhonotus* thus seems to represent a condition transitional, as regards shape of pupil, between the eyes of most diurnal vertebrates, which have round pupils, and those of many nocturnal forms which have vertically elliptical pupils and highly extensible irises.

The coloration is highly variable. As a rule the ventral surface is light, sometimes unicolor and sometimes with dark markings arranged in more or less well defined longitudinal bands (there are transverse markings on the chin in some forms). On the dorsal surface the ground color is usually marked with transverse dark bands, in which the posterior scales are tipped with white, especially on the sides of the body.

Juveniles of all but one of the forms examined differed strikingly from adults in color pattern, but closely resembled one another, indicating that their common pattern scheme is a retained ancestral one. In lizards having this pattern scheme there is a pale, broad, longitudinal band which includes the top of the head, the eight middorsal scale rows of the back, and the dorsal side of the tail, and which may be golden-brown, tan, or cream color. This pale dorsal color contrasts sharply with the dusky or gray color on the sides of the head, body, and tail. Spaced at intervals there are paired dots down the middle of the back, which represent the blotches usually present in adults. On the sides of the body vertical dark bars whose scales are tipped with white are prominent in young as in adults. The adult pattern is attained early in life; when the individual is less than half grown. In *Gerrhonotus coeruleus principis* the adult pattern closely resembles the juvenal pattern of all the forms here considered. It seems probable that in this race the basic ancestral pattern is retained with little modification. In all the other forms studied, the juvenal color pattern undergoes extensive modification during the early stages of growth. Usually the actual color changes, and the ground colors of the

sides and back become alike. In *G. coeruleus palmeri* the pattern tends to be suppressed, giving way to a monotone color effect. In *multi-carinatus* and related species, there is a tendency for transverse bands to form across the dorsal surface. In several forms heavy dorsal pigmentation not present in small juveniles is found in larger ones.

Secondary sexual characters are not striking. In immature specimens and in many adults the sex cannot be surely determined from external appearance. Males evidently attain somewhat larger size since the largest individuals of each form examined were males. In large adult males the head is noticeably swollen across the temporal region in correlation with the enlargement of the powerful jaw muscles. The scales are thickened and more heavily keeled in old males. The tail of the male is relatively thicker at its base than is that of the female. No differences in scalation between the sexes could be found in any of the forms studied. There may be average differences between the sexes in certain scale characters—especially in numbers of transverse rows on dorsal and ventral surfaces or in numbers of caudal scale whorls—which could be shown in a large series from a given locality. However, it seems evident that if such differences exist they are slight in comparison with individual and geographic variation. In view of this fact, and since the numerous subadults and juveniles are difficult to sex (this cannot be done without mutilating the specimens), males and females have not been separately dealt with here in showing geographic variation in the small series usually available.

Ordinarily the sexes show no differences in color pattern. However, in *G. m. multi-carinatus* of the San Francisco peninsula females are more often heavily pigmented with dark blotches than are males, which latter usually show more red in the coloration.

When adults of opposite sex are compared, males give the impression of being shorter-bodied and longer-limbed than females, and this difference can be confirmed by actual measurement, though it is slighter than had been anticipated and in itself will not serve as a basis for sexing of individuals. In a series of 20 male and 17 female *Gerrhonotus multi-carinatus webbii*, all adults from San Diego County, California, the averages of ratios of limb measurements to head and body length were as follows:

	hind leg	hind foot
males	.335	.150
females	.317	.143

Perfect tails varied in length in the specimens examined, and the number of caudal scale whorls varied from a maximum of 146 in *G. m. webbii* to as few as 86 in *G. c. principis*. In specimens which have had the tail broken early in life and regenerated, the original and regenerated parts are difficult to distinguish. Scales on the regenerated part are slightly smaller and less regularly arranged; they are less heavily keeled, and often they show a tendency to fuse. When only a few of the terminal segments are lost, they are not regenerated, and often it is doubtful whether all are present.

When a new tail begins to grow out, it has a covering of thin smooth skin; scales form later. For two adjacent whorls there is but a single caudal

vertebra. Normally the tail breaks through the middle of a vertebra hence it can be broken only between paired whorls of scales.

Experimentally the tail of one individual was cut off at an odd number of segments above a former break—between two caudal vertebrae at a point where a break would not normally have occurred. When the new tail appeared, it was beneath the posterior half of the last vertebra and this was pushed outward and finally shed, as the new tail grew.

As in other lizards the caudal vertebrae are replaced by a rod of cartilaginous tissue in the regenerated tail. Breaks seldom or never occur across the regenerated part of the tail, for it is tough and fibrous offering no weak points. If, experimentally, a cut is made through the regenerated tail, the end is inert and shows none of the lively reflex contractions which are ordinarily made by the freshly broken tail of a lizard, since the spinal cord is not regenerated. If, as nearly always happens under natural conditions, the regenerated tail is snapped off a few segments above the original break, the whole undergoes lively contractions. The regenerated part participates because it is innervated by branches of the caudal part of the spinal cord from the last segment anterior to it.

NUMBER OF SCALE WHORLS IN PERFECT TAILS

	Number of specimens	Average	Extremes
principis (entire range)	11	92.5	(86-100)
shastensis (SW Oregon)	15	98.8	(93-104)
shastensis (Trinity, Shasta, Tehama and Butte cos., California)	13	104.8	(93-110)
shastensis (Humboldt and Mendocino cos., California)	27	101.3 ± .6	(93-107)
shastensis (Sonoma Co., California)	14	109.5	(103-115)
coeruleus (Marin Co., California)	10	108.6	(102-116)
coeruleus (San Francisco peninsula)	17	102.7	(94-108)
palmeri (entire range)	17	100.2	(90-111)
scincicauda (entire range)	18	118.2	(115-123)
multi-carinatus (Sacramento Valley)	5	123.4	(121-132)
multi-carinatus (San Francisco Bay region)	12	121.6	(118-134)
multi-carinatus (Monterey to Ventura cos., California)	7	127.0	(121-134)
multi-carinatus (Santa Barbara Islands)	3	121.0	(116-124)
webbii (southern Sierra Nevada)	3	119.3	(116-125)
webbii (Los Angeles and San Bernardino cos.)	9	133.9	(125-142)
webbii (San Jacinto Mts. region)	4	125.2	(120-128)
webbii (San Diego Co.)	25	132.6 ± .8	(124-146)
webbii (Sierra San Pedro Martir)	9	125.2	(118-135)
nanus (Coronados Islands)	8	133.9	(128-142)
kingii (entire range)	4	123.5	(121-126)

Characters Used in Distinguishing Species and Subspecies

Because of the great range of individual variation, which obscures the trend of characters except when large series are compared, and the usual lack of large series, *Gerrhonotus* is a difficult genus to study. A number of populations which show marked average differences from other populations have not been recognized herein as distinct subspecies because of this variability.

Head and body length (measured from tip of snout to back of thigh) is used as an indicator of size.

The transverse dorsal scale rows were counted from just behind the ear opening to the row which extended to or overlapped the back of the thigh. The rows of right and left sides often do not meet evenly along the mid-dorsal line and there may be more rows on one side than on the other. To avoid confusion they were recorded always for one side only, the right, along the middle of the back. Former workers have sometimes recorded this scale count from the interoccipital plate to the back of the thigh. By adding two to the counts recorded in my paper they may be made equivalent to the results obtained by that method.

The transverse ventral rows were counted along the mid-ventral line from the mental plate to the preanal plates, inclusive. The longitudinal dorsal scale rows were counted across the middle of the body.

Scale whorls on the tail were counted from the first one behind the thigh to the tip of the tail.

In determining the proportion of keeled rows on the upper arm, the five rows were examined which showed greatest degree of keeling, if keels were present at all. Granular scales on the back of the arm were not counted. Likewise five rows were examined for keeling on the forearm.

On the tail the proportion of keeled to smooth scales was obtained by counting the scales on the first whorl toward the base where the total amounted to twenty. This method has advantages over Van Denburgh's method, of counting on the whorl five rows behind the anus, in that the uniform total makes ratios easier to express and granular scales present on the side of the tail near its base are eliminated from consideration.

Among the forms studied, variations in the number of the scales which were keeled, and in the degree of their keeling, were found to constitute important differences. Unfortunately, the degree of keeling cannot be measured directly. If they are not keeled, the scales are often convex and rounded. The keel, if it is present at all on a scale, may be so faint that it is difficult to perceive. Thus, in many specimens, I had arbitrarily to decide whether or not to call a row keeled.

The number of ventral longitudinal scale rows on the body was found to be constant, except in a few abnormal specimens which, in places, had the usual number of 12 increased to 13 or 14.

Although the shape of the head seemed strikingly different in different forms, measurements did not show these as clearly as was anticipated. Differences in sex and age apparently obscure such subspecific differences as do exist. The loosely articulated skull allows for some modification in the shape of the head according to the way in which any individual has been preserved. It may have hardened in a flattened or in a compressed form. In measurement of the body and limbs the same difficulty is encountered.

In descriptions of color, Ridgway's (1912) nomenclature has been employed.

Comparison of Gerrhonotus multi-carinatus and Gerrhonotus coeruleus

Gerrhonotus multi-carinatus attains a much larger average and maximum size than does *G. coeruleus*. Among specimens of the former species seen by me the maximum head and body length was 170 mm., while length in the largest *G. coeruleus* examined was under 135 mm. In *multi-carinatus* the head, body and tail are relatively slenderer, and the tail when perfect is more than twice the head and body length, whereas in *coeruleus* the head and body length is more than half the length of the tail. The number of whorls of scales on the tail is greater in *multi-carinatus* (usually more than 114) and smaller in *coeruleus* (usually less than 114). The greater tail length in *multi-carinatus* is probably correlated with the more marked climbing proclivities of this species which promote utilization of the tail as a prehensile organ.

The most convenient character for separating individuals of the two species is eye-color. The natural color of the eye is not apparent in preserved specimens and probably for that reason this character has escaped the notice of previous writers. In *multi-carinatus* the iris of the eye is yellow and devoid of dark pigment, so that blood vessels may be seen within it. In *coeruleus* the iris is pigmented, especially around the margin of the pupil. Often the pigmentation is so extensive that the whole eye appears black.

In *multi-carinatus* the dark dorsal markings are arranged in fairly regular transverse bands. In *coeruleus* dark markings, if present at all, are either in the form of spots or blotches, or, in heavily pigmented specimens, they are arranged in an irregular pattern and never are disposed in transverse bands sufficiently distinct to be counted. In *multi-carinatus* the white markings on the sides are in fairly regular rows, each of which is confined to the scale tip on one or two transverse rows of scales. In *coeruleus* these white markings are more scattered and some appear on almost every transverse scale row.

While the coloration is variable in both species, there are fairly constant differences. *G. coeruleus* is of more polished or glazed appearance than *multi-carinatus*, and its dorsal ground color has an olive, greenish, or bluish suffusion lacking in *multi-carinatus*, which tends to be more yellow or brown.

In *multi-carinatus* the dorsal scales are normally in fourteen longitudinal rows on the body. In occasional individuals the lateral rows are reduced to granules on each side so that only twelve full-sized rows remain. In the closely related species, *paucicarinatus*, there are usually sixteen, but the scales of the lowest row on each side are smaller than those of the rows above them. In *coeruleus* there are usually sixteen rows, but two subspecies show a tendency toward reduction of this number: *principis* by reduction in size of the lateral rows, and *coeruleus* by dropping out of the median rows on the back.

The interoccipital plate may or may not be divided in *coeruleus*, but in *multi-carinatus* it is normally single. The azygous prefrontal is always large and broad in *multi-carinatus* but in *coeruleus* it is often reduced and enclosed by the paired prefrontals and the internasals. In adults of *coeruleus* the scales on the sides of the tail are always keeled. In *multi-carinatus* these scales are usually smooth except in the race *webbii*.

Table showing trends of scale characters in *Gerrhonotus multi-carinatus* and *Gerrhonotus kingii*.

	Number of specimens	Average number of transverse dorsal scale rows	Extremes	Standard deviation	Coefficient of variability	Average number of transverse ventral scale rows	Extremes	Standard deviation	Coefficient of variability
scincicauda (entire range)	42	46.3 ± .2	(50-43)	1.40	3.02	66.1 ± .3	(69-62)	1.62	2.45
multi-carinatus (Sacramento Valley)	45	46.2 ± .2	(50-43)	1.55	2.27	65.4 ± .3	(70-62)	1.72	2.63
multi-carinatus (San Francisco Bay region)	69	46.5 ± .2	(50-43)	1.58	3.40	64.6 ± .2	(68-61)	1.67	2.59
multi-carinatus (Monterey to Ventura cos.)	25	47.2 ± .4	(50-42)	1.94	4.12	63.6 ± .4	(67-60)	1.86	2.93
multi-carinatus (Santa Barbara Islands)	12	46.0	(48-44)			63.5	(66-60)		
webbii (Southern Sierra Nevada)	30	44.4 ± .3	(48-42)	1.79	4.04	64.4 ± .3	(68-61)	1.59	2.47
webbii (Los Angeles and San Bernardino cos.	38	44.1 ± .2	(49-42)	1.45	3.29	63.4 ± .2	(67-60)	1.27	2.00
webbii (San Jacinto Mts. region)	20	44.4 ± .4	(48-41)	1.76	3.98	63.5 ± .4	(66-61)	1.58	2.50
webbii (San Diego Co.)	67	42.7 ± .2	(47-38)	1.75	4.10	63.3 ± .2	(67-60)	1.64	2.59
webbii (Sierra San Pedro Mártir)	44	41.5 ± .3	(45-38)	1.70	2.56	63.2 ± .3	(66-60)	1.64	2.53
nanus (Coronados Islands)	30	41.8 ± .2	(44-39)	1.20	2.87	60.8 ± .3	(65-58)	1.54	2.54
webbii (San Martín Island)	8	40.0	(41-39)			60.5	(62-58)		
kingii (entire range)	23	54.6 ± .3	(60-48)	2.71	4.96	67.4 ± .2	(74-62)	2.24	3.33

In general color pattern, arrangement of head scales, and relatively long tails, *G. paucicarinatus, G. cedrosensis, and G. kingii* resemble *multi-carinatus* rather than *coeruleus*. Eye color of these three southern species is unknown to me, because I have observed no living individuals.

Gerrhonotus multi-carinatus scincicauda (Skilton)

(Oregon alligator lizard, California lizard, horse lizard, rattlesnake lizard)

Tropidolepis scincicauda Skilton, 1849, p. 202 (original description).
Elgaria grandis Baird and Girard, 1852, p. 176.
Elgaria scincicauda, Baird and Girard, 1853, p. 348, pl. 4, figs. 1-3.
Gerrhonotus grandis, Cope, 1875, p. 46.
Gerrhonotus multicarinatus, Cope, 1875, p. 46 (part).
Gerrhonotus coeruleus, Boulenger, 1885, p. 273 (part).
Gerrhonotus scincicauda, Van Denburgh, 1912, p. 157.
Gerrhonotus scincicauda scincicauda, Grinnell and Camp, 1917, p. 166 (part).
Gerrhonotus multi-carinatus scincicauda, Fitch, 1934 b, p. 173.

Type.—Evidently young (total length given by Skilton as from 5 to 5½ inches; dorsal transverse bands represented by spots on the back and sides); collection of A. J. Skilton (present whereabouts unknown); The Dalles, Wasco County, Oregon; obtained from the Reverend G. Gary.

Diagnosis.—Size of adults large (head and body length more than 100 mm.); transverse dark bands on body black, a single scale row in width; no red in pattern; no dark spots on head; scales on lateral fold Cinnamon; upper two rows of temporals slightly keled or smooth, lower rows always smooth; scales of upper arm always smooth; eight dorsal rows keeled on tail; lateral and ventral caudals all smooth.

Range.—Includes interior valleys between the Coast Range and the Cascades, in Oregon, extending into southern Washington, and eastward along the Columbia River into north-central Oregon; northern and eastern limits of range imperfectly known; occurs west of inner Coast Range in northern California in interior valleys of Mendocino County. Van Denburgh gives (1922, p. 453) two Washington localities in Klickitat County; north side of Columbia River opposite mouth of John Day River, and 3 miles north of Grand Dalles. The United States National Museum has Oregon specimens from 7 miles north of Lonerock, Gilliam County, and Deschutes River. (See Figs. 1, 4.)

Description.—A living adult male, taken at The Dalles, Wasco County, Oregon, served for the following description.

Top of head and back, Old Gold blending into Cinnamon in granular area along sides; anterior supralabials Reed Yellow with no dark markings; twelve black bars on each side of body, each a single scale row in width, edged with white posteriorly, and extending up four rows from the lateral fold; black bars on each side connected by irregular dark bands, a single scale row in width crossing the back; these bands indistinct and suffused with the yellowish ground color, disappearing on tail a short distance behind its base; upper sides of legs and feet Old Gold, granular area on posterior side of thigh Cinnamon, ventral surface of body, legs, and tail dusky white. Iris yellow with no dark pigment.

Comparisons.—Differs from *G. m. multi-carinatus,* adjacent to the south, in absence of red from coloration, absence of dark pigmentation on top of head and on labials, smoothness of scales of upper arm, and fewer rows keeled on forearm and tail.

Variation.—Throughout the extensive range of this race there is notable constancy in all characters. No geographic trends are perceptible to me in size, color, pattern, scalation, or degree of keeling of scales, though there is, of course, some individual variation in each of these characters. Within the neighboring race *multi-carinatus,* however, there is marked geographic variation in each of these characters. Two of six topotypes of *scincicauda* from The Dalles (Calif. Acad. Sci. no. 30517; Mus. Vert. Zool. no. 15136) show a reduction of the first longitudinal scale row on each side, so that the scales are less than half the size of those of the rows above them. In two (Mus. Vert. Zool. nos. 15136 and 15138) the upper postnasal of the anterior pair is lacking on each side. The number of dorsal scale rows from behind the ear to the back of the thigh varied from 43 to 49; ventral scale rows from chin to anus varied from 63 to 69. There are never more than two rows of keeled scales on the forearm and all are smooth in many specimens. Coloration varied but little.

The largest specimen examined (Mus. Vert. Zool. no. 15130 from Jackson County, Oregon) was 141 mm. in head and body length. All others which appeared to be adults measured over 100 mm.

Gerrhonotus multi-carinatus multi-carinatus Blainville

(Red-backed alligator lizard; many keeled lizard)

Cordylus (Gerrhonotus) multi-carinatus Blainville, 1835, p. 57 (original description).
Gerrhonotus Wiegmanni Gray, 1845, p. 54.
Elgaria scincicauda, Girard, 1858, p. 210.
Gerrhonotus multicarinatus, Cope, 1875, p. 46.
Gerrhonotus scincicaudus, Cope, 1875, p. 47.
Gerrhonotus caeruleus, Boulenger, 1885, p. 273 (part).
Gerrhonotus scincicauda, Van Denburgh, 1897, p. 103 (part).
Gerrhonotus scincicauda scincicauda, Grinnell and Camp, 1917, p. 166 (part).
Gerrhonotus multi-carinatus multi-carinatus, Fitch, 1934 b, p. 173.

Type.—Specimen figured by Blainville (1835, pl. 5, fig. 2); Paris Museum; "Californie" (probably from vicinity of Monterey); P. E. Botta.

Diagnosis.—Size and scale characters in general the same as for *G. m. scincicauda;* a median row of red blotches on the back; top of head often mottled with dark markings; muzzle blunt; upper two rows of temporals convex and bluntly keeled or smooth; anterior pair of postnasals small; posterior pair of internasals reduced, usually not meeting medially; one to three rows of scales on the upper arm weakly keeled in adults; eight dorsal rows distinctly keeled on tail near its base with sometimes one or two additional rows keeled on each side.

Range.—Confined to California where it occurs in the Sacramento Valley and hills surrounding it (up into the yellow pine belt), the San Francisco Bay region, and thence southward along the coast to Ventura County. (See Fig. 1.)

Description.—The following color description was made March 31, 1933, from a living adult male (Mus. Vert. Zool. no. 16385) taken on the day before at Daly City, San Mateo County, California. Ground color Olive-Ocher; all plates on top of head heavily mottled with black; body in front of hind legs crossed dorsally by 10½ dark bands each involving 3½ to 5 transverse scale rows; on the sides the sequence of color is as follows for each band: zone of ground color half a scale row in width, zone of Cinnamon-Drab 1½ to 3½ (usually 2½) rows in width, zone of black confined to single transverse scale row, white markings confined to posterior edges of same scales which are black, except on the fourth and fifth longitudinal scale rows above

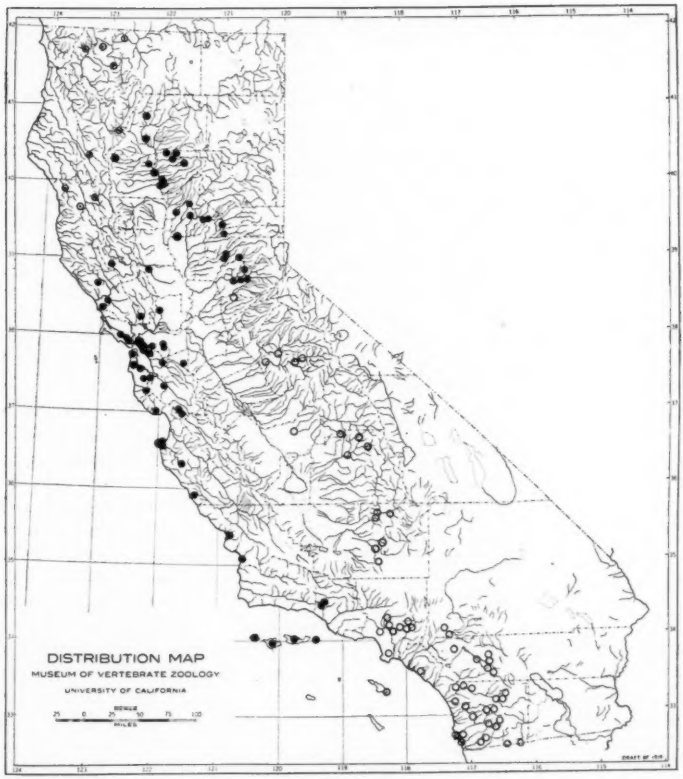

Fig. 1. Map showing localities in California represented by specimens examined of *Gerrhonotus multi-carinatus:* circle with dot, *G. m. scincicauda;* solid circle, *G. m. multi-carinatus;* open circle, *G. m. webbii.*

lateral fold, where they are more extensive and form indentations anteriorly; bands continuous across the back where they become black with conspicuous anterior borders of Brazil Red one or two rows in width; white markings inconspicuous on back and mostly confined to mid-dorsal region; lateral fold Light Drab on side of body, becomes Avellaneous in neck and thigh regions, has two longitudinal rows of white spots, those of the ventral row placed alternately to those of the dorsal row; eyelids Light Drab with Salmon-Orange borders; supralabials Pale Smoke Gray with black margins on posterior and inferior sides; a dark temporal stripe; limbs Olive-Ocher dorsally with black spots; tail spotted with black on sides, marked dorsally like the back, having black bands bordered anteriorly with Brazil Red; ventral surface of body and tail Pallid Neutral Gray with faint dusky lines bisecting the longitudinal scale rows; regenerated end of tail Ecru-Olive dorsally, paler ventrally; iris yellow with no dark pigment.

Comparisons.—Differs from the race *scincicauda* mainly in coloration and pattern, frequently having red markings on the back which are never present in *scincicauda,* often having dark spots or mottling on the head, in having the dark bands on the body frequently widened and more regularly arranged. Differs also in scalation, having on the average, slightly fewer transverse ventral scale rows, and slightly longer tails with more whorls of caudal scales. Also in *multi-carinatus* usually some of the lateral caudal scales are faintly keeled in addition to those of the eight mid-dorsal rows which alone are keeled in *scincicauda.* In *multi-carinatus,* on the average, more than one row of scales are keeled on both the upper arm and the forearm whereas in *scincicauda* all scales of the upper arm are smooth and not more than one row on the forearm is keeled. The upper temporal scales tend to be more frequently and more distinctly keeled in *multi-carinatus* than in *scincicauda.* Differs from the race *webbii* in size, body proportions, color pattern, and degree of keeling of scales. Average head and body length for 13 adults from San Mateo County is 123 mm., maximum 133 mm., in contrast to measurements of 33 adult *webbii* from San Diego County in which the average head and body length is 135 mm., maximum 166 mm. Muzzle blunter and relatively shorter in *multi-carinatus.* In *webbii* the tail averages longer and has a greater number of scale whorls and caudal vertebrae. *G. m. webbii* ordinarily has no red in the coloration although in occasional specimens it is conspicuous. Rarely individuals of *webbii* are heavily pigmented and have dark blotches on the head, but are never as dark as are extreme examples of *multi-carinatus.* In *webbii* the transverse dark bands on the body are deeply indented with conspicuous white markings in the middle of the back and on the fifth scale above the lateral fold on each side. In *multi-carinatus* these indentations may be present but much less conspicuous. On the average in *multi-carinatus* fewer rows of temporal, upper arm, forearm, and caudal scales are keeled and the keels are fainter. Although it cannot be measured, difference in degree of keeling results in a marked difference in the appearances, of the animals. The occipital plates are not keeled in *multi-carinatus* but usually are sharply keeled in *webbii.*

Variation.—The description given above applies only to specimens taken in San Francisco and San Mateo counties. Some specimens from this area show less red and more black in the pattern than the one described, although all show some red and usually it is the most noticeable feature of the pattern. On the average, females have less of the red coloring and more of the black than do males. Specimens from the Sacramento Valley are here included with *multi-carinatus*. They are highly variable and intermediate in some respects between *scincicauda,* and *multi-carinatus* of the San Francisco peninsula, therefore they could not in my judgment be defined properly as a separate subspecies. They show about the same amount of variation in different parts of this area, and, in color pattern at least, none is typical of either *scincicauda* or *multi-carinatus*. This population is here included with *multi-carinatus* rather than with *scincicauda* because the latter shows uniformity in its characters over a wide area while the former everywhere shows a wide range of variation, and typical specimens occur within only a relatively small area.

The following color description, which would apply to many individuals from the Sacramento Valley, was taken, April 19, 1932, from a living adult female collected on April 2, 1932, 6 miles south of Los Molinos and across the county line in Butte County, California (Mus. Vert. Zool. no. 15143): top of head Olive-Yellow, unspotted; back and upper sides of front limbs paler; fourteen transverse bands across sides and back; their posterior parts black for the width of a single scale row; each black scale edged posteriorly with white, the white markings becoming indistinct on the four mid-dorsal rows; black bands straight and of uniform width, not broken or V-shaped, each blending anteriorly on the back into Ochraceous-Tawny which in turn blends into the lighter ground color; hind legs ochraceous dorsally; ventral surface dull white.

Numerous other specimens from widely separated localities in the Sacramento Valley have red blotches on the back but the red in such specimens is usually paler and less sharply set off from the ground color than it is in typical specimens. In these northern specimens the dark transverse bands across the body are broad and regularly arranged, and on the back each blends from black along its sharply defined posterior edge to brownish, chestnut, or red anteriorly, becoming gradually paler and more diffuse, and blending into the ground color. The body pattern of broad, regular bands in these specimens somewhat resembles that of *kingii*. All from this general region are recognizable as distinct from *scincicauda,* and nearly all are likewise distinguishable from typical *multi-carinatus*. Hence this Sacramento Valley population might be considered a distinct race, but the pattern differences are not entirely constant, or at least not always discernible to me, and no associated structural differences have been found. Therefore such subdivision seems to me inadvisable. Heavily pigmented individuals occur only near the coast, eastward as far as Napa and Solano counties, and from Contra Costa and San Francisco counties southward. The most heavily pigmented specimens examined were from Alameda and Contra Costa counties. In some of these the transverse dark bands are so wide that the ground color is almost obscured, and

there are dark blotches on all the cephalic plates. Heavily pigmented specimens which have no red on the back usually show faint reddish or orange coloring at the angle of the jaw and on the eyelids.

A series of over twenty specimens from the vicinity of Palo Alto, Santa Clara County, is atypical in that none is heavily pigmented and none has conspicuous red markings. Most of the specimens examined from Monterey County are heavily pigmented and have red dorsal blotches. A half-grown specimen from Monterey (Calif. Acad. Sci. no. 13677) is unique in being uniform dark brown dorsally with no trace of the usual dark markings on the ground color. A juvenile (Calif. Acad. Sci. no. 50481) from Sespe Creek, Ventura County, is similar to it in appearance and shows only faint traces of the transverse bands. Most of the specimens that were examined from San Luis Obispo County were heavily pigmented, and in life probably showed some red in the dorsal coloration. Specimens from Marin, Sonoma and Lake counties are referred to *multi-carinatus* because some show keeling of the upper arm scales and red in the dorsal coloration. None of those examined from Marin and Sonoma counties was heavily pigmented. There is a general tendency for keeling of scales to become progressively more pronounced and extensive toward the southern part of the range in *multi-carinatus*. Thus Sacramento Valley specimens have an average of 1.1 humeral rows keeled, those from the counties immediately east of San Francisco Bay 1.5 rows, those from the San Francisco peninsula, 1.8 rows and all those from more southern parts of the range average 2 rows. This variation is closely paralleled throughout by increased keeling of the forearm scales. Series from north of San Francisco Bay average 1.5 rows of keeled temporals on each side of the head, those from Alameda and Contra Costa counties have 1.9 keeled rows and those from farther south 2.0 rows. Series from the San Francisco peninsula depart from the general trend in showing almost complete lack of keeling of the temporal scales. In keeling of caudal scale rows the same trend can be traced with an increase of from 8.7 rows in Sacramento Valley specimens to 10.5 rows in those from Ventura County.

Systematic Remarks.—O'Shaughnessy (1873: 45), writing of the type specimen of *Gerrhonotus wiegmanni* in the British Museum, noticed its similarity to figures of *Elgaria grandis*. Van Denburgh (1897, p. 103; 1922, p. 450) doubtfully included this older name in the synonymy of *Gerrhonotus scincicauda*.

Through the kindness of Mr. H. W. Parker, of the British Museum, who has reëxamined the type at my request and compared it with representative specimens of Pacific Coast forms sent by me, I have been able to obtain fairly conclusive evidence of the identity of the central Californian form of *multicarinatus* with *G. wiegmanni*. Mr. Parker writes of the type that it was taken by the botanist George Barclay on the voyage of the "Sulphur" around the world during the years 1835-41. The expedition stopped in the San Francisco Bay region from October 20 to November 30, 1837. During this stay a trip was made up the Sacramento River as far as the mouth of the Feather River, and the Santa Clara Valley and other points in the San Francisco Bay

region were visited. Four days, from December 2 to 6, were spent at Monterey. No other localities within the known range of *Gerrhonotus* were visited. Several points along the west coast of Mexico and Central America were touched on the voyage, but it seems highly improbable that the type could have been taken in that region since all the southern forms of *Gerrhonotus* seem to be restricted to high altitudes in the interior.

Some of Mr. Parker's remarks concerning the type are here quoted:

> The species certainly seems to be the same as your '*scincicauda*' [the name under which *multi-carinatus* was then known]. There are 14 dorsal scale rows and the interoccipital is undivided; but the white spots of the sides are rather irregularly arranged and, further, extend right across the back, very much as in the specimen of '*G. caeruleus*' said to be from Cartago, Costa Rica, and figured by Günther in the Biologia Centr. Americana, Rept., Pl. XXV, fig. D.
>
> It does not agree exactly . . . . [either with a specimen of *scincicauda* from Oregon or with a specimen from San Mateo County, California, showing extreme development of the red blotches]. The upper arm and temporal scales are quite smooth, there is no red colouring and the head is uniform. But 10 dorsal scale rows at the base of the tail are keeled. It seems to me that, unless there really is another form in the Costa Rican region, *wiegmanni* takes precedence over *scincicauda* and typical *wiegmanni* is the same as typical *scincicauda*.

All characters of the type of *wiegmanni* thus fall within the range of variation of the Californian form *multi-carinatus*, and the name *wiegmanni* is therefore definitely disposed of, as a synonym of *multi-carinatus*.

The absence of red blotches in the coloration, and the absence of dark markings on the head, in the type of *wiegmanni* may be taken as evidence that it did not come from the San Francisco peninsula, since all specimens examined by me from that area show one or both characters. However, the red fades after preservation and might disappear entirely. It is only the presence of these distinctive characters in specimens from the San Francisco peninsula which justifies the separation of the central Californian form *multi-carinatus* from its northern and southern races; in most other characters it is intermediate. The type of *wiegmanni* was thus probably somewhat intermediate toward *scincicauda* and came from either the north side of San Francisco Bay or the lower Sacramento Valley.

Gerrhonotus multi-carinatus webbii (Baird)

(San Diego alligator lizard)

Gerrhonotus webbii Baird, 1858, p. 255 (original description).
Gerrhonotus scincicaudus, Yarrow and Henshaw, 1878, p. 1641 (part).
Gerrhonotus multicarinatus, Cope, 1883, p. 29.
Gerrhonotus scincicauda, Stejneger, 1893, p. 196.
Gerrhonotus scincicauda ignavus Van Denburgh, 1905, p. 19.
Gerrhonotus scincicauda webbii, Grinnell and Camp, 1917, p. 168.
Gerrhonotus scincicaudus webbii, Stephens, 1921, p. 62.
Gerrhonotus multi-carinatus webbii, Fitch, 1934 b. p. 173.

Type.—Young; U. S. Nat. Mus., no. 3078; "San Diego to El Paso," probably from near vicinity of San Diego, San Diego County, California [?], Dr. T. H. Webb of U. S. and Mexican Boundary Survey Commission; April or May, 1852 [?].

Diagnosis.—Size large (head and body length of old adults usually more than 130 mm.); dorsal scales all heavily keeled; dark transverse bands on body deeply indented with white markings on fifth scale row above lateral fold on each side and in middle of back; upper two rows of temporal scales heavily keeled; lower rows weakly keeled or smooth; three or more rows of scales on upper arm distinctly keeled, eight dorsal scale rows of tail heavily keeled, several rows on each side of tail weakly keeled; tail relatively long and slender; muzzle long and pointed.

Range.—Includes the Sonoran Life Zone of the west slope of the Sierra Nevada from Amador County southward, and extends southward through cismontane California and the San Pedro Mártir Mountains of northern Lower California. (See Figs. 1, 2.)

Description.—The following color description was taken September 19, 1932, from a living adult female collected near Glendale, Los Angeles County, California: top of head, sides of body, and lateral fold Drab-Gray; temporal and labial regions paler; labials edged with black on their upper margins; eighth supralabials darker than the ones anterior to it and contrasting to color of the third infraocular and posterior supralabials which are almost white; loreal and postnasals faintly edged with black posteriorly; lower side of upper arm and granular region on back of thigh ochraceous; upper surfaces of front limbs Drab-Gray; a row of spots along the lateral fold which are irregular in size and arrangement, some tinged with Ochraceous-Orange, the remainder white; granular scales on soles of feet and around anus Ochraceous-Orange; ten black transverse bands between occiput and back of thigh, each a single scale row in width but usually crossing to the next anterior row on the fourth scale above the lateral fold, and sometimes two scale rows in width at the point of overlapping; each transverse band deeply indented with white posteriorly on the fifth scale row above the lateral fold on each side and on the middle of the back; ventral surfaces shiny gray, with traces of ochraceous on tail and hind limbs; regenerated tail Dark Neutral Gray; iris yellow with no dark pigment.

Variation.—A specimen from Plymouth, Amador County (Mus. Vert. Zool. no. 15148), is doubtfully included with *webbii* because of its large size, prominent keeling of two scale rows on the upper arm and keeling of lateral caudal scales, and conspicuous white indentations of the transverse dark bars. In most respects, however, it is intermediate between the Sacramento Valley population of *multi-carinatus* and typical *webbii*. It resembles the former in having a blunt muzzle bluntly keeled upper temporals and short tail (117 whorls).

Two specimens from the coast of Ventura County (exact locality not recorded), are arbitrarily referred to *webbii*. Both have dark blotches on the head and one (Stanford, no. 5236) has the transverse bands two rows wide shading anteriorly into chestnut, which may have been red in life. The lower temporals are smooth and the upper two rows only weakly keeled, but twelve rows of dorsal caudals are keeled. Intergradation between *multi-carinatus*

and *webbii* seems to occur in the central Sierra Nevada and in Ventura County.

Rarely, specimens of *webbii* have red in the dorsal coloration. Three (Calif. Acad. Sci. nos. 57330 from Alcatraz, Lower California, 40299 from Campo, San Diego County, and 58148 from Pala, San Diego County) show as much red as examples of *multi-carinatus* from the San Francisco peninsula.

Specimens from Los Angeles County and more southern localities are uniform in appearance and on the average show a gradual increase in the degree of keeling and number of rows keeled farther southward. Mus Vert. Zool. no. 8099 taken near Colton, San Bernardino County, is abnormal in having a regenerated tail which forks into four approximately equal branches about half an inch behind its origin from the old tail. Mus. Vert. Zool. no. 3583 from Pasadena has a double regenerated tail.

Southern Sierra Nevada specimens differ from typical *webbii* in having shorter tails and have on the average fewer scale rows keeled, of temporals (2.2 as opposed to 2.4), upper arm (3.7 as opposed to 3.9), forearm (2 as opposed to 2.6), and caudals (11.3 as opposed to 13.5). They are variable in color pattern. Several have small, dark blotches on the plates of the head. Mus. Vert. Zool. no. 2859, from Bodfish, Kern County, is heavily pigmented. having broad transverse dorsal bands. Several are much larger than any of the subspecies of *multi-carinatus* examined; Mus. Vert. Zool. no. 10191 from Big Creek, Kern County, was the largest *Gerrhonotus* examined by me; it had a head and body length of 170 mm. Series from Los Angeles County and from the San Bernardino and San Jacinto mountain regions are intermediate. as regards extent of keeling of temporal, upper arm, forearm, and caudal scales, between Sierra Nevada specimens and typical *webbii* of San Diego County. The trend toward increased keeling farther south continues into Lower California and culminates in the San Mártin Island population having keeled 4 rows of temporal and upper arm scales 3 rows on the forearm, and 14.3 rows on the tail. Other characters of *webbii* which tend to become more pronounced toward the southern end of its range are the narrow pointed shape of the muzzle and the pale ground color often tinged with orange or ochraceous.

Gerrhonotus multi-carinatus nanus Fitch

(Coronados alligator lizard)

Gerrhonotus scincicauda [*ignavus?*], Van Denburgh, 1905, p. 18.
Gerrhonotus scincicauda ignavus, Van Denburgh and Slevin, 1914, p. 140.
Gerrhonotus scincicauda webbii, Van Denburgh, 1922, p. 459.
Gerrhonotus scincicauda nanus Fitch, 1934 a, p. 7 (original description).

Type.—Adult male, Mus. Vert. Zool. no. 5402; July 1, 1913; South Island, Los Coronados Islands, Lower California, Mexico; A. B. Howell.

Diagnosis.—Size small (maximum head and body length among 79 specimens 114 mm., average 93.3 among 49 evidently adult); upper two rows of temporals sharply keeled, lower rows weakly keeled or smooth; muzzle pointed; one to three rows of scales on upper arm weakly keeled in adults; eight dorsal

rows of caudal scales strongly keeled on tail near its base, two or three rows of lateral caudals usually keeled on each side. Number of transverse scale rows reduced in both dorsal and ventral series especially ventrals (average 60.4); dark ventral longitudinal lines conspicuous in adults, dark brown in color, transverse bands on body dark brown; a wide dark brown stripe extending across temporal region from eye to ear.

Range.—Los Coronados Islands (North, Middle, East, and South), Lower California, Mexico. (See Fig. 2.)

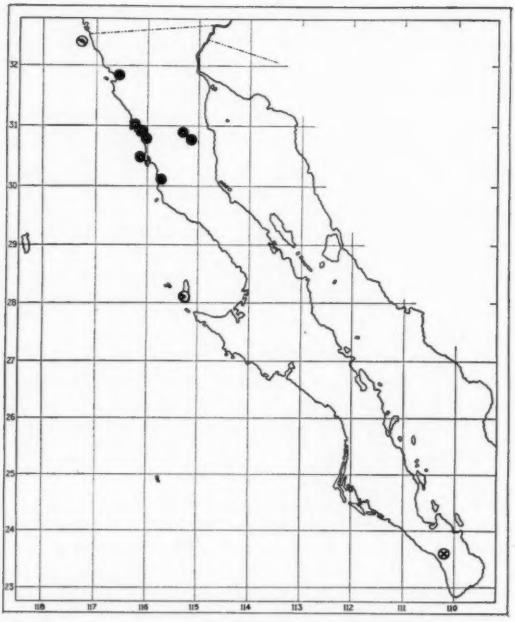

Fig. 2. Map showing localities of *Gerrhonotus* examined from Lower California, Mexico: open circle, *G. multi-carinatus nanus;* solid circle, *G. multi-carinatus webbii;* circle with dot, *G. cedrosensis;* circle and cross, *G. paucicarinatus.*

Comparison.—Differs from the race *webbii* in much smaller size (this form being actually the smallest of the species), less extensive carination of scales, and smaller number of transverse scale rows, and, to a lesser degree, in color pattern. Average head and body length for 49 adults 93.3 mm., maximum 114 in contrast with measurements of 35 adult *webbii* from San Diego County in which the average is 135 mm., maximum 166. On the average *nanus* has fewer upper arm and lateral caudal scales keeled and the keeling is fainter. While in most adults of *webbii* the dark ventral longitudinal lines are faint,

or have disappeared altogether, in *nanus* they are usually conspicuous and are of a deep brown color instead of the slate gray usually seen in other forms. On the dorsal surface *nanus* is usually more heavily pigmented than *webbii*, has a conspicuous temporal stripe and often has the top of the head mottled with brown. The transverse dark bands on the body are usually dark brown in color. There is an average difference in the number of transverse ventral scale rows as shown in the following table:

Number of transverse ventral scale rows from chin to anus	57	58	59	60	61	62	63	64	65	66	67
G. w. nanus, % among 79 specimens from Los Coronados Islands	3.8	8.9	19	25.3	21.5	11.4	7.6		2.5		
G. w. webbii, % among 73 specimens from San Diego County				8.2	8.2	19.2	23.3	20.6	13.7	4.1	2.7

In numbers of dorsal and ventral scale rows *nanus* agrees closely with the San Martín Island population of *webbii*, which also differs from typical *webbii* in having numbers of these rows reduced. This San Martín Island population has not been included with *nanus* because it differs in other characters; carination of scales is heavier than in any other population of *Gerrhonotus* studied, in contrast with the relatively smooth scales of *nanus;* size is larger than in *nanus,* though smaller than in typical *webbii* (could not be accurately determined with the few specimens available); brownish ventral lines in adults, and occasional dark spots on head less developed than in *nanus*. When large series of this San Martín Island population become available for study making possible an accurate analysis of its characters, its subspecific separation from *webbii* may seem advisable. In this event the subspecific name *ignavus* is available for it.

To what extent adult size is influenced ontogenetically by the direct effect of the environment upon the individual, and to what extent it is genetic has not been determined. It is evident that there is a wide range of variation in adult size and that growth continues after breeding maturity is attained. However it seems probable that adult size is largely determined by genetic factors which differ in populations, and that the average adult size and normal size range within populations is constant. The largest individuals differ from juveniles and small adults in having relatively thicker, more heavily keeled scales and, in males, heads much swollen in temporal region. The largest individuals examined of the small form, *nanus*, showed these characters presumably indicative of advanced age even though they were smaller than small adults of typical *webbii*.

Variation.—No distinct racial tendencies showing differences between the populations of the different islands could be found. In a few specimens the mid-dorsal markings on the body were reddish as in *multi-carinatus*. Ten of the 79 specimens examined showed a tendency toward reduction of the normal number of 14 longitudinal scale rows to 12.

Gerrhonotus cedrosensis Fitch

(Cedros Island alligator lizard)

Gerrhonotus cedrosensis Fitch, 1934a, p. 6 (original description).

Type.—Adult male, Calif. Acad. Sci. no. 56187, July 23, 1923; Cedros Island, Lower California, Mexico; J. R. Slevin.

Diagnosis.—Size, smaller than any form of the species *G. multi-carinatus;* lateral fold white with gray or black reticulations; 14 longitudinal dorsal scale rows; 10 dorsal rows of scales weakly keeled on the body; 8 dorsal rows weakly keeled on upper side of tail near its base; dorsal scales of neck smooth; temporals and occipitals smooth and rounded; scales on sides of body smooth; all scales on fore and hind limbs smooth; number of transverse dorsal scale rows between ear and back of thigh less than 50.

Range.—Known only from three specimens, Calif. Acad. Sci. nos. 56187, 59577 and 59578, collected July 23, 1923; June 3 and 5, 1925, respectively, all taken by J. R. Slevin on Cedros Island, Lower California. (See Fig. 2.)

Comparisons.—Differs from *multi-carinatus* in details of scalation. In the three Cedros Island specimens, all of which are evidently adults, the scale rows on the upper side of the thigh are smooth while in the San Lucan form these rows are distinctly keeled. In *cedrosensis* the dorsal scales of the neck region are all smooth while in *multi-carinatus* they are weakly keeled. All *multi-carinatus* examined had 50 or more dorsal scale rows, while the maximum was 48 and the average 46.6 in the three specimens of *cedrosensis*. It is probable that if larger series of *cedrosensis* and of typical *multi-carinatus* were compared, a certain amount of overlapping would be found in this character. In *cedrosensis* the dark ventral lines are faint; in *paucicarinatus* they are distinct and tend to be broken up into series of dots which are sharply outlined. In view of its isolation, both in distance and in faunal barriers, from *multi-carinatus* of the Cape Region, the resemblance of *cedrosensis* to that form is striking. The occurrence of any alligator lizard on Cedros Island is surprising.

In number of transverse dorsal scale rows the present form is intermediate between typical *paucicarinatus* and *G. multi-carinatus webbii* of northern Lower California, it might thus be thought to show intergradation between the two species. Apparently this is not the case. *G. m. webbii* shows progressively heavier keeling of the scales and fewer dorsal rows toward the southern end of its range so that individuals geographically nearest to *cedrosensis* are farthest removed structurally. Again, *cedrosensis* is less heavily keeled than is *paucicarinatus*.

Variation.—All of the three specimens examined have 14 longitudinal dorsal scale rows, and have 45 to 48 transverse dorsal scale rows (average 46.6); 62 to 63 ventral scale rows (average 62.3); tail composed of 107 to 117 whorls of scales from behind thigh to tip; two pairs of postnasals on each side.

In two specimens, the type and no. 59578, the color pattern is the same as that of *paucicarinatus* but in the third, no. 59577, the dark transverse bars are almost obsolete.

Gerrhonotus paucicarinatus Fitch

(San Lucas alligator lizard)

Gerrhonotus multicarinatus, Dumeril and Bibron, 1839, p. 404.
Gerrhonotus multi-carinatus, Stejneger and Barbour, 1917, p. 61.
Gerrhonotus paucicarinatus Fitch, 1934b, p. 173 (original description).

Type.—Adult male; Mus. Vert. Zool. no. 11768; Todos Santos, Lower California, Mexico; C. C. Lamb, October 29, 1928.

Diagnosis.—Close to *G. cedrosensis* in size and coloration; granular area of lateral fold white crossed by narrow black bars; alternate black and white markings on both upper and lower labials; 16 or 14 longitudinal dorsal scale rows, with eight rows on the back moderately keeled forming continuous longitudinal ridges, lower rows faintly keeled; eight dorsal rows keeled on tail near its base; four internasals of about the same size, the right and left member of each pair broadly in contact along the median line; temporal scales all smooth; lateral and ventral caudals smooth; scales of upper arm and forearm smooth: two rows on upper side of thigh keeled; scales on anterior and lateral sides of tibia keeled; about fifty transverse dorsal scale rows between ear and back of thigh.

Range.—*G. paucicarinatus* is found only at high altitudes in the Cape Region of Lower California. (See Fig. 2.)

Description.—The following description was made from the type (in alcohol): head, back, and tail, Ecru-Olive dorsally; sides of body above lateral fold Light Mouse Gray; upper sides of fore and hind legs Ecru-Olive with several black, white-tipped scales on thigh; body crossed dorsally by eleven dark transverse bands between occiput and back of thigh which, on the sides, are straight and two scale rows in width and have the upper third of each scale in the posterior row white; no white markings on back, where the bands become narrower, irregular, and angular; top of head faintly spotted with black; alternate black and white markings on labials giving side of face a striped appearance from lateral view; a faint dark bar across temporal region from behind eye; granular area of lateral fold white, crossed by narrow irregular black lines which are continuous with transverse bands of body.

Comparison.—*G. paucicarinatus* differs from *G. multi-carinatus webbii* in number and degree of keeling of its scales, in size, in bodily proportions, and in color pattern. All the dorsal scales are much more heavily keeled in *webbii* giving the animal a rougher appearance. Scales of the upper arm, forearm, sides of the tail, and temporal region which are smooth in *paucicarinatus* are prominently keeled in *webbii*. There are 16 longitudinal rows of dorsal scales in the majority of specimens of *paucicarinatus* but only 14 (or rarely 12) of these rows in *webbii*. There are 50 or more transverse dorsal scale rows in *paucicarinatus*, not more than 44 in *webbii* from northern Lower California. In *paucicarinatus* the muzzle is narrower and more pointed than in *webbii* and as a result the internasals of each side are forced together and have wider contact medially. There is probably no overlapping in size between the two forms as adults of *webbii* are well over 100 mm. in head and body length. All *pauci-*

carinatus examined were less than 100 mm. in length. A young specimen (Calif. Acad. Sci. no. 46724) taken August 15, 1919, has a head and body length of 29 mm., thus is smaller than the young of *G. coeruleus* at birth or those of *G. multi-carinatus* at the time of hatching. In *paucicarinatus* the lateral fold is white with narrow black lines. In *webbii* as in other subspecies of *multi-carinatus* the ground color of the body predominates on the lateral fold and there are scattered white spots but no black markings. In *paucicarinatus* the labials are banded with alternate black and white markings, in *webbii* they are unicolor or the supralabials may be faintly edged with black. In *paucicarinatus* the ground color is more coppery or russet, less yellow than in the races of *multi-carinatus*.

Variation.—Of the ten specimens examined three had only 14 longitudinal dorsal scale rows, the others each had 16. In three there were 50 transverse dorsal rows between ear and back of thigh; each of the other seven specimens had 51 rows. The ventral rows from chin to anus varied from 60 to 64 with an average of 62.7. There were 11 or 12 dorsal bands on the body. The dark ventral lines are within the longitudinal scale rows (as in *multi-carinatus)* but are faint and broken into a series of dots in most of the specimens.

Gerrhonotus kingii (Gray)

(Sonoran alligator lizard)

Elgaria Kingii Gray, 1838, p. 390 (original description).
Gerrhonotus multifasciatus Dumeril and Bibron, 1839, p. 401.
Elgaria nobilis Baird and Girard, 1852, p. 129.
Elgaria marginata Hallowell, 1852, p. 179.
Gerrhonotus nobilis, Baird, 1859, p. 11.
Gerrhonotus kingii, O'Shaughnessy, 1873, p. 46.

Type.—Adult; Brit. Mus. Nat. Hist., "a"; "Mexico"; presented by Thomas Bell. (This information furnished by Boulenger, 1885, p. 275; no type specimen, type locality, or collector mentioned in original description. Original description evidently made by Bell, as indicated by the citation, as a synonym, of "*Gerrhonotus Kingii*, Bell MSS" immediately following the caption *Elgaria Kingii).*

Diagnosis.—Size medium (head and body length of adults about 100 mm.); usually longitudinal dorsal scale rows, 6 or 8 weakly keeled on middle of back; temporals, occipitals, dorsal scales of neck and those of upper arm, forearm, and thigh all smooth; usually more than 50 transverse dorsal scale rows; granular area of lateral fold dull gray; series of broad transverse bands dorsally on neck, body, and tail; alternate black and white markings on labials; tail almost encircled by dark bands.

Range.—Mountains in southeastern Arizona, southwestern New Mexico and in adjacent parts of Chihuahua and Sonora, northern Mexico. (See Fig. 3.)

Description.—An adult specimen (Mus. Vert. Zool. no. 13846) from the Mexican boundary had the following color pattern (in alcohol):

Dorsal ground color of head Deep Olive-Buff, paling on body and tail to Olive-Buff tinted with Chamois, marked with series of transverse dark bands, first just behind ear opening, each occupying about three transverse scale rows, intensified, black and sharply defined along irregular anterior and posterior borders, paler and browner (Buckthorn Brown) in center, gradually blending laterally into Vinaceous Buff of sides; these bands separated by pale areas about equal to the length of 1½ dorsal scales. Series of black scales with white tips on sides of body, these arranged in regular rows with three or four rows intervening, confined to three rows immediately above lateral fold on

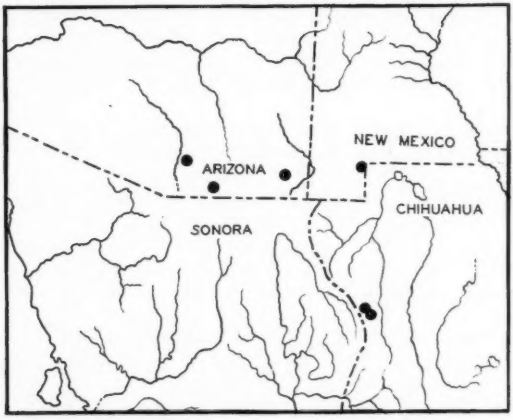

Fig. 3. Map showing localities of specimens examined of *Gerrhonotus kingii* in Arizona, New Mexico, and Chihuahua.

each side; top of head heavily mottled with dark brown, spots situated mainly in corners or along edges of cephalic plates. Anterior supralabials all heavily marked with dark brown or black posteriorly; conspicuous dark mark beneath eye, separated from another on penultimate supralabial and lower temporals by intervening white area. Rows of black, white-tipped scales low on sides of tail, similar to those on sides of body, and joining dark dorsal bands nearly to encircle tail. On three ventral scale rows nearest lateral fold on each side, at intervals, scales are heavily marked with black which tends to form bars corresponding to those on sides above lateral folds. Granular area of lateral fold dull gray. Ventral surface dull white, heavily speckled with black on tail, and on body along edges of lateral fold.

Comparisons.—Gerrhonotus kingii appears to be closely related to *G. multi-carinatus*, from which it differs mainly in weaker and less extensive keeling of its dorsal scales, paler ground color, and broader dorsal bands. It differs also in having a greater number of transverse dorsal scale rows, and there is

but little overlapping between the two species in this character; the ventral rows are also more numerous in *kingii*. This high number of scale rows is correlated with the elongate shape of the body in *kingii*, which has relatively smaller and weaker limbs and feet than has *multi-carinatus*.

Gerrhonotus kingii differs from *multi-carinatus* in several characters in which it resembles *paucicarinatus* and evidently the latter species is its nearest relative. *G. paucicarinatus* is smaller than *kingii*, averages fewer transverse dorsal and ventral scale rows and fewer whorls of caudals, has faint keels on dorsal scales of neck and limbs which are smooth in *kingii*, has, on the average, more longitudinal dorsal scale rows (usually 16 rather than 14), and has narrower, less regularly arranged, dorsal bands, which, on the back are black rather than brown. In increased numbers of dorsal and ventral scale rows, reduction in keeling of scales, and in alternate black and white markings on labials, *kingii* and *paucicarinatus* resemble each other but differ from *multi-carinatus*.

Variation.—In the 23 specimens examined, numbers of dorsal bands on the body varied; eight had nine bands, nine had ten, and six had eleven. In original description it is stated that the type specimen has 16 longitudinal dorsal scale rows. This specimen was stated by Boulenger *(loc. cit.)* to have come from Mexico. Of the specimens examined by me, all those taken north of the international boundary had only 14 full-sized rows, though in one from Ramsey Canyon, Huachuca Mountains, Arizona, granules of the lateral fold were enlarged to form an additional row of half-sized scales on each side. However, the only Mexican specimen examined by me (from Colima Garcia, Chihuahua) had only 16 rows of scales. This is evidence that the species may be differentiated into northern and southern populations differing in numbers of scale rows.

Gerrhonotus coeruleus principis (Baird and Girard)

(Northern alligator lizard)

Elgaria principis Baird and Girard, 1852, p. 175 (original description).
Gerrhonotus principis, Cope, 1875, p. 46.
Gerrhonotus grandis, Yarrow, 1883, p. 47 (part).
Gerrhonitus caeruleus, Boulenger, 1885, p. 273 (part).
Gerrhonotus principis, McLain, 1899, p. 9.
Gerrhonotus coeruleus, Van Denburgh, 1922, p. 422 (part).
G[*errhonotus*] c[*oeruleus*] *principis*, Fitch, 1934 a, p. 6.

Type.—Apparently none was designated from among the original specimens collected by the United States Exploring Expedition in 1841; type locality "Oregon and Puget Sound."

Diagnosis.—Size small (head and body length of adults less than 100 mm.); a light mid-dorsal longitudinal band on back 6 or 8 scale rows in width contrasting to darker coloring of sides; iris of eye dark, pigmented; dorsal scales in 14 full-sized longitudinal rows often with an additional row of smaller scales on each side; dark ventral lines when present running between longitudinal scale rows, usually indistinct in adults; scales on back and sides of body

Table showing trends of scale characters in populations of *Gerrhonotus coeruleus*.

	Number of specimens	Average number of transverse dorsal scale rows	Extremes	Standard deviation	Coefficient of variability	Average number of transverse ventral scale rows	Extremes	Standard deviation	Coefficient of variability
principis (British Columbia and Washington)	10	45.8	(43-48)			60.9	(58-64)		
principis (Oregon Coast)	25	45.5 ± .4	(42-49)	1.96	4.31	61.6 ± .5	(58-67)	2.24	3.63
principis (Del Norte Co., California)	14	44.4	(42-49)			60.0	(57-64)		
shastensis (Jackson Co., Ore.)	32	47.9 ± .3	(44-51)	1.64	3.43	64.7 ± .3	(61-67)	1.80	2.78
shastensis (Humboldt and Mendocino cos., California)	42	45.4 ± .4	(39-50)	2.42	5.33	61.8 ± .3	(57-66)	2.12	3.43
shastensis (Siskiyou and Trinity cos., California)	24	45.2 ± .3	(42-49)	1.58	3.50	62.9 ± .5	(60-67)	2.08	3.30
shastensis (Shasta, Tehama and Butte cos., California)	34	44.2 ± .3	(42-48)	1.48	3.35	61.8 ± .4	(58-66)	2.16	3.50
shastensis (Sonoma Co., California)	22	45.5 ± .4	(43-49)	1.68	3.69	61.3 ± .4	(58-64)	1.76	2.87
coeruleus (Marin Co., California)	11	45.4	(41-49)			62.4	(59-65)		
coeruleus (San Francisco peninsula, California)	71	44.7 ± .2	(41-52)	1.89	4.23	60.9 ± .2	(56-64)	1.98	3.25
palmeri (southern Sierra Nevada)	53	41.8 ± .3	(38-46)	2.15	5.15	61.3 ± .3	(58-65)	1.64	2.67

weakly keeled, scales on upper arm and forearm smooth or with one or two rows weakly keeled; temporal scales smooth; scales of medial rows of neck three to six rows behind interoccipital plate broader than long and broader than scales lateral to them; dark markings on back small scattered spots or absent; no white-tipped scales on back; no transverse bars on dorsal side of tail, dark markings when present there consist of small, rounded, median blotches, and occasionally series of lateral blotches well separated from the median ones; head triangular and flattened with blunt muzzle; body flattened; tail short (less than $1\frac{1}{2}$ times head and body length with fewer than 100 whorls); cephalic plates flattened; anterior and posterior pairs of postnasals typically present on both sides; azygous prefrontals usually small, rhomboidal, enclosed on each side by posterior internasal and paired prefrontal separating it from postnasals; frontoparietal hexagonal with sides parallel, and with anterior and posterior ends nearly symmetrical; usually 3 interoccipitals, a larger median plate and a pair of smaller laterals symmetrically arranged.

Range.—British Columbia east to western Montana, western Washington, western Oregon, California Coast as far south as Humboldt County. Van Denburgh (1922, pp. 438, 439) records *principis* from Sicamous and Kaslo, in British Columbia; Lower Kootenay River, Easton, New Whatcom, San Juan Islands, Port Townsend and Gorse Creek, in Washington; and from Seaside, Portland, Vida, Empire, and Marshfield, in Oregon. There is one in the National Museum from Rock Creek, Montana. (See Figs. 4, 5.)

Description.—An adult female (Mus. Vert. Zool. no. 15106) from Hunter Creek, Curry County, Oregon, had a light mid-dorsal band involving $6\,{}^{2}/_{2}$ longitudinal scale rows on body, Dark Olive-Buff, gradually blending into Light Neutral Gray on head but changing abruptly to Light Neutral Gray on sides; lateral fold Light Neutral Gray with indistinct light spots, irregular black spots scattered over back on dorsal band, and occupying $^{1}/_{3}$ or more of its total area; spots centering on edges and corners of scales; limbs Light Neutral Gray dorsally; ventral surfaces of body limbs and tail Pallid Purplish Gray with slight concentration of pigment at lateral edges of scales.

Comparisons.—In *principis* the dark color of the sides (brownish gray or sooty) contrasts with brown (pale tan to rich golden brown) of back. The ground color is never greenish or bluish, as it often is in the other races. Black scales on sides are more numerous than in other races of *coeruleus* and occur on nearly every transverse scale row but are scattered and inconspicuous because of predominantly dusky color of sides. White tips on scales of sides minute, completely lacking in some individuals. Black markings on top of head often absent and seldom conspicuous, mainly confined to edges of scales rather than centers as in *shastensis*, contrasting sharply with paler ground color, not blending with it as in *coeruleus*. A dark temporal streak, and often a black spot in loreal region, but no conspicuous labial markings; labials beneath and anterior to eye often have a few inconspicuous, irregular, black marks on their lower portions along edge of mouth. Series of small median blotches down back sometimes paired, each blotch usually smaller than a single

Table showing trends of scale characters among the subspecies of *Gerrhonotus coeruleus*.

Locality	Number of specimens	Total number of postnasals %					Number of interoccipitals %		
		4	5	6	7	8	1	2	3
British Columbia (mainland) and Washington	8					100		12	88
Oregon coast	15		6.6	33.3	33.3	26.8			100
Del Norte and Humboldt counties	40	17.5	15	20	12.5	35	58	13	28.7
Mendocino County	27	22		33		45	31	28	41
Sonoma County	34	23.5	17.5	14.7	14.7	28.4	23.3	30	46.7
Marin County	15	53.3	26.7	20			7.7	53.8	38.5
San Francisco and San Mateo counties	70	68.6	14.2	8.6	4.3	4.3	15.9	23.8	60.3
Santa Cruz County	4	25	25	25	25			25	75
Monterey County	10	50	40		10		12.5	37.5	50
Jackson and Klamath counties, Oregon	37			24.3	16.2	59.5	37	18.5	44.5
South Fork and Yolla Bolly mountains	41	2.4		2.4	7.2	88	66	11.3	22.5
Lassen region	28	3.5				96.5	100		
Sierra Nevada	51				11.7	88.3	84.4	5.8	9.8

scale. In unusually heavily pigmented individuals there are several other series of small blotches on either side of this median series, but all blotches are small and sharply defined. Blotches continue along midline on to tail, but do not form transverse bars on tail as in *shastensis;* in heavily pigmented individuals, however, there may be lateral tail blotches on either side of the median ones but well separated from them.

Table showing trends of scale characters among the subspecies of *Gerrhonotus coeruleus*

	Number of specimens	Medial dorsal scale rows		Azygous Prefrontal		
		% Fuse with lateral rows	% Do not fuse	% In contact with postnasals on both sides	% in contact with postnasals on one side only	% Completely enclosed by paired prefrontals and internasals
British Columbia (mainland) and Washington	8		100			100
Oregon coast	15		100	20	20	60
Del Norte and Humboldt counties	40		100			
Mendocino County	27		100	52	14.7	33.3
Sonoma County	34	3	97	53	17.6	29.4
Marin County	15	40	60		14.5	85.5
San Francisco and San Mateo counties	70	71.8	28.2	2	18	80
Santa Cruz County	4	50	50			100
Monterey County	10		100			
Jackson and Klamath counties, Oregon	37		100	37.5	17.5	45
South Fork and Yolla Bolly Mts.	41		100	100		
Lassen Region	28	2.4	97.6	100		
Sierra Nevada	51		100	100		

Variation.—Dorsal scale rows varied from 42 to 51 in specimens examined. Ventral rows varied from 57 to 67. In some specimens the longitudinal rows on each side just above lateral fold are only slightly smaller than the upper rows; in others the scales of these rows are reduced to granules. No definite geographic trends are apparent in either of the foregoing characters.

In four specimens from western Washington presumably typical, as well as in three from the Lillooet River Valley, British Columbia, there are two pairs of postnasals on each side. In two of the Washington specimens the postnasals show a tendency to break up into granules. In the majority of specimens from the southern Oregon coast the number of postnasals is re-

duced and muzzle seems to be blunter and deeper than in typical individuals of *principis;* they thus resemble typical *coeruleus* in both these characters. Since these specimens are widely separated from the range of typical *coeruleus,* the resemblance is probably less indicative of relationship than of parallelism. Of two from Vancouver Island each has only a single pair of postnasals on each side. More material is needed to ascertain whether this reduction is constant in Vancouver Island specimens, and whether two pairs are always present in Washington specimens. There is a wide range of variation in the amount of pigmentation on the light dorsal band but, insofar as could be determined, it has no correlation with geographical distribution or even with local conditions. Three from near Bandon, Coos County, Oregon (Mus. Vert. Zool. nos. 15100, 15103 and 15104) have all the temporal scales bluntly but distinctly keeled, whereas in all others they are smooth.

Gerrhonotus coeruleus shastensis Fitch

(Shasta alligator lizard, redwood lizard)

Gerrhonotus coeruleus shastensis Fitch, 1934a, p. 6 (original description).
Gerrhonotus principis, Van Denburgh, 1897, p. 112.
Gerrhonotus burnettii, McLain, 1899, p. 9.
Gerrhonotus coeruleus, Grinnell and Camp, 1917, p. 169 (part).
Gerrhonotus palmeri, Grinnell, Dixon and Linsdale, 1930, p. 146.

Type.—Adult male, Mus. Vert. Zool. no. 15047; June 27, 1932; meadow on south side of Burney Creek, 3000 feet, two miles southwest of Burney, Shasta County, California; H. S. Fitch.

Diagnosis.—Resembles *G. c. principis* in most respects but differs from it as follows: size large (head and body length 90 to 133 mm. in adults); no light mid-dorsal band contrasting to color of sides in adults; ground color of head and neck often paler than that of body and contrasting with it; ground color brown, bluish, greenish, or yellowish, often obscured by heavy pigmentation on dorsal surface; dark scales of body and tail often white-tipped; dark scales with white tips on sides scattered, not arranged in regular transverse rows; dark markings usually present on dorsal side of tail, arranged in transverse bands half encircling tail; dorsal scales in 16 full-sized rows; scales on back and sides of body moderately keeled; cephalic plates only moderately flattened; azygous prefrontal large, in contact with postnasals on both sides, rounded anteriorly, pointed posteriorly, and concave on posterior sides; interoccipitals 1, 2, or 3, variable in size and shape, usually unsymmetrically arranged; frontoparietal wider posteriorly than anteriorly, its sides concave.

Range.—Intergrades with *principis* in southwestern Oregon and extends southward through the Siskiyou, Trinity, Mount Shasta, Yolla Bolly, South Fork and Sanhedrin mountain ranges, reaching the coast in Humboldt County and extending southward to northern Sonoma County where it intergrades with *coeruleus.* On the east side of the Sacramento Valley it extends southward to the Lassen Peak region where it intergrades with *palmeri,* and eastward to the Warner Mountains (specimens in Mus. Vert. Zool. from Twelve-mile Creek, Modoc Co., Calif. at Nevada line). (See Figs. 4, 5.)

Fig. 4. Map showing records of occurrence of *Gerrhonotus* in British Columbia, Washington, and Oregon. Open circles show published records of *G. coeruleus principis;* solid circles show specimens examined of *G. coeruleus principis;* open triangles show published records of *G. multi-carinatus scincicauda;* solid triangles show specimens examined of *G. multi-carinatus scincicauda;* circles with dots show specimens examined of *G. coeruleus shastensis.*

Description.—Taken September 18, 1932, from a living adult female captured near Burney, Shasta County, on June 27, 1932: top of head and neck Bluish Glaucous blending into Citron Green on the body; dorsal surface of limbs, head and body heavily pigmented; dark markings tend to form regular bars on every other transverse scale row on sides, but have no definite arrangement on back where they blend and almost obscure ground color; a dark stripe across temporal region behind eye; dark longitudinal stripes on regenerated part of tail; ventral surfaces of limbs, body and tail dull white.

The newborn young of this female were banded dorsally with Tawny-Olive with a row of small black mid-dorsal dots; on the sides they showed various shades of gray, with white-tipped scales.

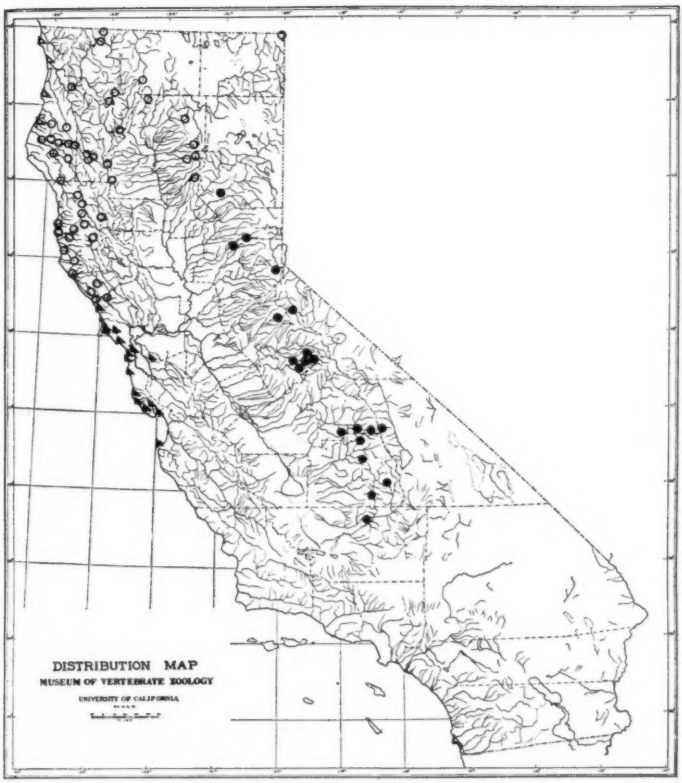

Fig. 5. Map showing localities in California represented by specimens examined of *Gerrhonotus coeruleus;* open triangle, *G. c. principis;* open circle, *G. c. shastensis;* solid circle, *G. c. palmeri;* solid triangle, *C. c. coeruleus.*

In an adult female taken at Grass Valley Creek, Trinity County, the ground color of the body was Buffy Citrine blending on the neck and head into Light Grayish Olive. The coloration was palest in the labial region. The whole ventral surface in this specimen was dull white, the scales suffused with dusky coloring. There were no dark spots on the head plates in this individual but pigmentation was present along the edges of the plates. In an individual of the light phase from Lyonsville, Tehama County, the following coloration was recorded: head and neck Light Celandine Green dorsally; body Mignonette Green dorsally contrasting with color of head and neck with abrupt transition; lateral fold Light Cadmium Yellow blending into Mignonette Green dorsally; a few scattered blackish white-tipped scales on sides anteriorly; none posteriorly; a few dark scales in middle of back and tail, these suffused with the ground color.

Variation.—Specimens from the southern part of the range in Mendocino and Sonoma counties show tendencies toward *coeruleus,* having the muzzle blunt and arched; frequently having the number of postnasals reduced; and having relatively small feet. In these specimens the azygous prefrontal averages smaller and narrower than in typical *shastensis* and is frequently enclosed on one or both sides by the paired prefrontals and posterior internasals, and the interoccipital often is divided. Specimens from the immediate vicinity of the coast in Mendocino County (Noyo River, Mendocino City, Gualala) seem to show a strong tendency toward *principis* both in coloration and scalation. Several have a distinct light mid-dorsal band with small scattered dark spots. In most of them the muzzle is deep and arched, the number of postnasals is reduced, and the azygous prefrontal is enclosed laterally by the paired prefrontals. Perhaps specimens from a narrow strip along the coast should be separated from those of the interior, which are more nearly typical, and should be included with *principis* or considered intergrades between *principis* and *coeruleus.* Only a few of these coastal specimens were available and they have been included with *shastensis* because this race appears to reach the coast in almost typical form farther north. In specimens from South Fork Mountain and the Yolla Bolly Mountains, the dark pigmentation is browner, less nearly black than in those of eastern Shasta County. South Fork Mountain and Yolla Bolly Mountain specimens often have the scales of the upper arm and forearm, and sometimes the temporals, distinctly keeled thus differing from specimens taken elsewhere.

Specimens from Jackson and Klamath counties, Oregon, are in almost every respect intermediate between *principis* and *shastensis,* and the Klamath County specimens are nearer *principis* than are those of Jackson County. They may be distinguished from typical *principis* by: large azygous prefrontals, in contact with postnasals; markedly concave sides of frontoparietal, which is widened posteriorly; heavier keeling of scales; sixteen full-sized dorsal scale rows; slightly longer tails; darker and richer brown dorsal ground color; lack of contrast between color of sides and back with no pale mid-dorsal band set off from lateral areas; white-tipped scales usually present on back. On the dorsal side of the tail the pattern is a combination of the rounded median

blotches found in *principis* and the transverse bars or half rings characteristic of the *shastensis* pattern, with the later usually predominating. The ground color of head and body often differ noticeably, though offering less contrast than usually found in more typical *shastensis*. The head plates are sharply outlined by pigmentation along the sutures separating them. Usually there are no dark blotches on top of the head, and when such blotches are present they are usually situated along sutures rather than in centers of cephalic plates.

Most of the specimens examined from the Lassen region are not heavily pigmented and approach *palmeri* in coloration, but differ in having the temporals smooth and more scales of upper arm and forearm smooth.

Gerrhonotus coeruleus coeruleus Wiegmann

(San Francisco alligator lizard, Spanish lizard)

Gerrhonotus coeruleus Wiegmann, 1828, p. 380 (original description).
Gerrhonotus Burnettii Gray, 1831, p. 64.
Elgaria formosa Baird and Girard, 1852, p. 175.
G(errhonotus) (Elgaria) formosa, O'Shaughnessy, 1873, p. 45.
Gerrhonotus grandis, Yarrow, 1883, p. 47 (part).
Gerrhonotus multicarinatus, Yarrow, 1883, p. 47 (part).
Gerrhonotus scincicaudus, Yarrow, 1883, p. 48 (part).
Gerrhonotus caeruleus, Boulenger, 1885, p. 273 (part).
Gerrhonotus burnettii, Van Denburgh, 1897, p. 107.
Gerrhonotus coeruleus coruleus, Fitch, 1934 a, p. 6.

Type.—Adult, Berlin Mus. Nat. Hist. no. 1163; October, 1816; San Francisco, California; A. von Chamisso.

Diagnosis.—In general resembles *G. c. principis* except as here specified: size small (head and body length usually less than 100 mm.); dorsal scales in 16 longitudinal rows, those of medial rows small and crowded or often in places lacking on one or both sides leaving total of 14 or 15 rows; scales on back and sides of body heavily keeled giving animal roughened appearance; scales of medial rows of neck 3 to 6 rows behind interoccipital plates longer than wide, narrower than scales of rows lateral to them; dark markings on back in form of large median blotches, or, less commonly, widened transversely into bands; dark areas on sides tend to be arranged in transverse bars with paler areas intervening; head and body relatively narrow and deep; muzzle blunt, arched in profile; tail of moderate length (usually more than $1\frac{1}{2}$ times head and body length with more than 100 whorls of scales); limbs small (length of hind foot less than $\frac{1}{7}$ of head and body length); plates on top of head thick with roughened surfaces separated by deeply incised sutures; number of postnasals reduced to totals of 4 to 6 (rarely 7 or 8); interoccipitals usually 2 or 3, often unsymmetrically arranged and of unequal sizes.

Range.—Narrow strip of Transition Life Zone along central California coast from southern Sonoma County to Monterey. (See Fig. 5.)

Description.—(Made from living adult male from Daly City, San Mateo County, California).

Top of head Olive-Brown with no distinct spots; Olive-Gray mid-dorsal band on back $6\,{}^{2}/_{2}$ rows in width; a dark bar on the side for three transverse rows of scales, each bar extending upward to middle of fifth row above lateral fold; posterior scale row of each bar Clove Brown tipped with white posteriorly, the Clove Brown blending to Olive-Brown and to Olive-Gray anteriorly; a row of large median Clove Brown blotches on back, each about 4 scales wide, its borders indistinct; no white-tipped scales on back; one or more white-tipped scales on every transverse scale row of body on sides; upper labials Olive-Gray with dark spots, upper surfaces of limbs Olive-Gray with ill-defined Clove Brown spots, an indistinct dark band across temporal region from behind eye; ventral surfaces of body, limbs and tail Pallid Purple-Drab with an iridescent luster, edges of scales paler.

Although the general pattern is similar in most specimens, the shades of color vary in different individuals. In others from the same locality as the specimen described above, the dorsal bands were Light Olive-Gray, Deep Olive-Gray, Light Cinnamon-Drab, Avellaneous, Pinkish Cinnamon, and a variety of other shades.

In *coeruleus* all of the dark markings on the dorsal surface have a stippled appearance and are not as sharply defined as they are in the other races. The dark pigmentation is broken up into small dots. The facial markings are characteristic; the loreal region is heavily marked with black; upper parts of suboculars are edged with black; usually three black blotches along supralabials, one anterior to eye, one just beneath eye, and one on penultimate supralabial. These facial marks have no well defined borders and apparently the pigment is laid down in general regions without respect to the position of scale boundaries, which they often cross.

Comparisons.—Typical *coeruleus* differs from *G. c. shastensis,* with which it intergrades in the north, in size, body proportions, scalation and color pattern. The average head and body length of adult *coeruleus* is less than 100 mm. and the largest specimen examined was 108 mm. adults of typical *shastensis* average over 100 mm. and the largest specimen examined (Mus. Vert. Zool. no. 14562) had a head and body length of 128 mm. In *coeruleus* the relative sizes of the limbs and feet are noticeably smaller; (hind foot less than $1/_{7}$ of head and body length whereas it exceeds this ratio in *shastensis).* In *coeruleus* the head is narrower and deeper; in *shastensis* the head and body are more flattened, and the muzzle is less arched in profile. In *coeruleus* the azygous prefrontal is small, quadrangular, and usually enclosed on one or both sides by the posterior internasals and the paired prefrontals; in *shastensis* it is large and has contact on both sides with the postnasals and the loreal. In *coeruleus* there is a strong tendency toward reduction of the number of postnasals so that a single pair remains on each side; in *shastensis* there are typically two pairs of postnasals on each side. In *coeruleus* the scales of the back are rougher and more strongly keeled, the medial rows are relatively narrower especially in the neck region, and show a tendency to drop out or fuse with the rows lateral to them. The plates on top of the head are thicker and rougher in *coeruleus.* Adults of *shastensis* do not show the light mid-dorsal

Table showing differences in body proportions in representative series of *coeruleus* from different parts of the range. All specimens measured were adult.

Locality	Number of specimens	Head and body length in mm.	Axilla to back of thigh: % of head and body length	Length of hind limb: % head and body length	Length of hind foot: % head and body length	Length of fore-limb: % head and body length	Length of fore-foot: % head and body length	Depth of muzzle: % head and body length
San Francisco, California (*coeruleus*)	17	88.9	63.9	30.6	13.6	22.4	9.9	6.0
Grass Valley Creek, Trinity County, California (*shastensis*)	17	108.8	63.2	36.9	18.1	27.4	12.0	5.6
Yosemite and General Grant National Parks, California (*palmeri*)	26	93.9	61.4	37.1	17.5	27.3	12.1	4.9
Rogue River, Curry County, Oregon (*principis*)	10	82.6	64.2	33.2	15.2	25.1	10.6	5.9

band which is characteristic of *coeruleus*. In *shastensis* the dark markings are more sharply defined on the ground color. *G. c. shastensis* shows greater extremes of pigmentation or lack of it, while the pattern is more uniform in *coeruleus*. In *shastensis* the ground color on the head and neck is often noticeably lighter than the ground color of the body and contrasts with it. In *coeruleus* the head is usually of a darker shade than the back.

Variation.—Specimens from Marin County show the peculiarities of this form, but less strongly than do those taken south of San Francisco Bay; on the average they are larger in size, they have more postnasals and they have the dorsal scales less heavily keeled. They show partial loss of the median dorsal rows less frequently. A specimen from Redwood Cañon, Alameda County (Mus. Vert. Zool. no. 5576) is the only one from the east side of San Francisco Bay. It is larger than most *coeruleus*, the mid-dorsal band is indistinct, the dorsal blotches are broken up, and the azygous prefrontal is large. In appearance it is most like specimens from Marin County.

More than 100 specimens which I examined from San Francisco and San Mateo counties showed a wide range of variation in details of scalation and color pattern, but in general appearance all were strikingly similar. Four specimens from Santa Cruz County (Ben Lomond, and 5 miles east of Big Basin) had unusually extensive dark pigmentation dorsally, so that the mid-dorsal blotches joined the bars of the sides and the dorsal band was almost obscured. The fact that these lizards all came from a heavily forested locality may have some correlation with their heavier pigmentation. Specimens of the small series (10) examined from Monterey County seemed to be typical except that the dorsal blotches were short and wide and tended to form transverse bars across the back connecting the dark areas of the sides, and none showed fusion of the dorsal scale rows. One specimen (Mus. Vert. Zool. no. 4808) is labeled "Santa Paula, Ventura County, locality doubtful." The locality is undoubtedly erroneous. The specimen is typical except that the dorsal blotches are small and faint, and the medial dorsal scale rows are unusually wide anteriorly.

Systematic Remarks.—In the original description of *Gerrhonotus coeruleus*, the type locality given was "Brasilia." Stejneger (1902, p. 37) has examined and identified the type and has shown that it was undoubtedly taken at San Francisco, as the collector, von Chamisso, collected there on his voyage around the world. In the original description the measurements, color description and scale characters mentioned all agree with individuals from the San Francisco peninsula.

The type of *Gerrhonotus burnettii* evidently came from Monterey, although the type locality given in the original description was "South America." The specimen was taken on the voyage of the "Blossom" and the two Californian ports visited by this ship were San Francisco and Monterey. Both stops at San Francisco were made in November and December when lizards probably would not have been active. Beechey (1831, p. 82) in his narrative of the voyage, after a detailed account of the birds and mammals in the vicinity of

San Francisco, says: "I shall pass rapidly over the reptiles which are not numerous and none were procured during our stay." *Gerrhonotus burnettii* is here included in the synonomy of *coeruleus,* since specimens from Monterey and from San Francisco agree closely in most characters.

The origin of the type of *Elgaria formosa* is less clear. This specimen (U. S. Nat. Mus. no. 4132) was taken in 1841 by the United States Exploring Expedition in "Upper California." San Francisco was the only port on the California coast touched by the expedition. Various parts of the Bay Region were visited. A party was sent into the interior but its explorations were confined to the Sacramento Valley and it did not come within the range of *coeruleus;* another party had traveled overland from Vancouver to San Francisco. It passed through regions inhabited by *G. coeruleus* in the Siskiyou Mountains and in the vicinity of Mount Shasta, but probably little collecting was done *en route* as the trip was a hurried one. From the description and figures of the type it seems evident that it did not come from extreme northern California. It agrees with typical *coeruleus* in having only one pair of postnasals on each side, in having the interoccipital divided into three plates, in having the snout blunt and the muzzle arched in profile. Since the ships of the expedition anchored at Sausalito, it is probable that the type was taken in Marin rather than in San Francisco County. The specimen figured by Girard (1858, pl. 23, figs. 10-17) does not show the characteristic color pattern of *coeruleus* but resembles certain specimens showing a minimum of pigmentation, which seemingly occur throughout the range of *coeruleus* but especially in Sonoma County. There is no evidence that members of the expedition collected in Sonoma County, and it is probable that the type represents an unusually pale individual from Marin County. Since the type of *Elgaria formosa* agrees closely with typical *coeruleus* in characters other than those of coloration, it is here included in the synonymy of that form.

I refer specimens from Marin and southern Sonoma counties to *G. c. coeruleus* despite the water barrier separating them from those of the San Francisco peninsula. These specimens from north of the Bay have the deep narrow head, blunt, arched muzzle, small feet, heavy keeling of dorsal scales with crowding and fusion of medial rows, reduced number of postnasals and light mid-dorsal band which are characteristic of typical *coeruleus.* Intergradation with *shastensis* is relatively abrupt and takes place almost entirely within Sonoma County. Lizards strongly showing the characters of typical *coeruleus* apparently are not found north of the Santa Rosa Valley.

Typical *coeruleus* may be regarded as an aberrant form possibly of insular origin. It may have evolved at a time when the Marin and San Francisco peninsulas were connected with each other but separated from the mainland. Evidence from the flora and from position of fault lines indicates that such conditions may have existed during the Pleistocene.

Crowding and fusion of the medial scale rows on the back, and their heavier keeling, seem to be correlated with a narrowing and deepening of the body. This modified body shape may be correlated with the lizard's habits.

Individuals discovered in their natural hiding places, usually under rocks, are almost invariably found tightly coiled with the tail folded around the side of the body, and the same position is also assumed by captive individuals, although they may not be beneath any object. This characteristic resting position seems to be peculiar to the subspecies *coeruleus* and is seldom or never assumed by individuals of the other races.

Reductions in the numbers of postnasals and supralabials and in the size of the azygous prefrontal seem to be the result of an increase in size and crowding backward of the rostral, nasal, and internasal plates correlated with a widening and deepening of the anterior end of the muzzle. The heavier jaw thus produced may be an adaptation for crushing the small, hard-shelled carabid beetles which figure importantly in its food. A lizard feeding upon more active prey might be expected to have a more pointed muzzle.

Gerrhonotus coeruleus palmeri Stejneger

(Sierra alligator lizard, snake lizard)

Gerrhonotus scincicauda palmeri Stejneger, 1893, p. 196 (original description).
Gerrhonotus principis, Van Denburgh, 1897, p. 112 (part).
Gerrhonotus palmeri, Van Denburgh, 1897, p. 113.
Gerrhonotous palmeri, Van Denburgh, 1898, p. 64.
Gerrhonotus multicarinatus palmerii, Cope, 1900, p. 525.
Gerrhonotus coeruleus palmeri, Fitch, 1934a, p. 6.

Type.—Adult male, U. S. Nat. Mus. no. 18606; 1891; South Fork of Kings River, Fresno County, California; T. S. Palmer.

Diagnosis.—Corresponds to *G. c. principis* except as here specified: size relatively large (head and body length of adults sometimes exceeding 100 mm.); ground color dull, brownish or olive, uniform on head, back, and sides; dorsal scales in 16 longitudinal rows; scales on dorsal surfaces of neck, body, and limbs sharply keeled; temporal scales keeled; three or more rows on upper arm and forearm keeled; rows on upper side of thigh keeled; scales of tibia keeled; scales on upper side of foot sometimes keeled; scales on sides of tail keeled; dark dorsal markings on ground color indistinct, often absent; white-tipped scales, if present at all, often on back as well as on sides; few and scattered, not arranged in regular transverse rows; head triangular and flattened with pointed muzzle; tail of moderate length (more than 1½ times head and body length with usually more than 100 whorls); cephalic plates only moderately flattened, with conspicuous sutures marked by dark lines; 2 pairs of postnasals on each side (8 in all); azygous prefrontal large, in contact with postnasals on both sides, rounded anteriorly, pointed posteriorly with posterior sides concave; frontoparietal narrower anteriorly, wider posteriorly, its sides concave; usually a single interoccipital, occasionally 2 or 3, which are of unequal sizes and unsymmetricalliy arranged; limbs well developed (hind foot $^1/_6$ or more of head and body length).

Range.—Restricted to the Sierra Nevada of California, mainly west slope, in Hudsonian, Canadian and Transition life zones. (See Fig. 5.)

Description.—The following color description was made, September 18, 1932, from a living adult male taken at Sand Flats, 6000 feet, Stanislaus River, Alpine County, California. Head, body and limbs Vetiver Green or Citrine-Drab dorsally, one or more black scales on every transverse row, each with a white spot, usually on posterior side; most of dark scales confined to sides; a few in mid-dorsal region appearing on every second or third row, fewer on tail, there showing tendency to blend with ground color; upper labials Clear Dull Green Yellow; abdomen Clear Dull Green Yellow laterally becoming dull white medially; a few dark, white-tipped scales on upper arm and dorsal side of thigh; granular ventral sides of legs Clear Dull Green Yellow; regenerated part of tail Dark Olive-Buff.

Comparisons.—*G. c. palmeri* differs from *shastensis,* adjacent to its range in the north, in color pattern and degree of keeling of its scales; to a lesser degree in size and body proportions. Typically *palmeri* has all the temporal scales keeled while in *shastensis* they are ordinarily smooth. Typical individuals of *palmeri* have all the scales of the upper arm keeled and have three or more rows keeled on the forearm. In *shastensis* there are usually not more than three rows of scales keeled on the upper arm nor more than two rows keeled on the forearm, and these keels are usually weak, sometimes altogether absent. The dorsal scales of the neck region are more heavily keeled in *palmeri.* The ground color is duller with less pigmentation in *palmeri* than in *shastensis.* There are seldom distinct dark spots on the head or a distinct dark band behind the eye in *palmeri* but these are characteristic of *shastensis,* except in extreme individuals of the light phase. In occasional heavily pigmented individuals of *palmeri* the ground color showing between the dark blotches is dull brown or gray, not yellow or green as it often is in *shastensis.* From unpigmented individuals of the light phase of *shastensis, palmeri* differs in having the head and neck of the same color as the body dorsally. In *shastensis* the head and neck are of a distinctly different color from the body, lighter, with an abrupt transition anterior to the forelimbs.

The average and maximum sizes of *palmeri* are distinctly smaller than those attained by *shastensis,* but individuals cannot be separated on the basis of size. The number of caudal whorls in several of the *palmeri* examined was less than 100 and the average is fewer than in *shastensis.* In *shastensis* the muzzle is deeper and the head is less flattened than in *palmeri.*

Variation.—Specimens from the Yosemite region are not typical. In several the temporal scales are all smooth and in the others they are only faintly keeled. The majority of the Yosemite specimens have only two rows distinctly keeled on the forearm. They average larger than specimens taken farther south. A specimen from Fallen Leaf Lake, Eldorado County (Mus. Vert. Zool. no. 7204), is heavily pigmented with large blotches on the dorsal surfaces of head and body. It shows no keeling of the arm, forearm, or temporal

scales. Several other specimens from the same locality are also smooth scaled and have a color pattern like that of *principis* with small scattered black spots on the back. An adult from Butte Meadows, Butte County, is typical of *palmeri* in coloration but has all the temporals and forearm scales smooth, hence is referred to *shastensis*.

Summary and Conclusions

In the region from British Columbia south through Lower California, and east to the Rocky Mountains the genus *Gerrhonotus* is represented by two major groups, the *coeruleus* group and the *multi-carinatus* group. These are in the main complementary in distribution, but their ranges overlap.

The *multi-carinatus* group includes four distinct species, widely separated from each other by physiographic and climatic barriers. The complex of forms here assembled under the specific name *multi-carinatus* has heretofore been currently regarded as consisting of only two races and for these the species name *scincicauda* has most generally been used. I have recognized four forms within this complex. Of these the northern race *scincicauda,* of south-central Washington, north-central and western Oregon, and northwestern California, is notably constant in all its characters throughout its extensive range, having a shorter tail than the other races, scales less extensively keeled, more transverse scale rows both dorsally and ventrally, and pattern lacking bright colors. The race *multi-carinatus* of west-central California is intermediate between *scincicauda* and the southern race *webbii* in scale characters and is variable in pattern, individually and geographically. Within its range are two seemingly well differentiated geographic populations which possibly are deserving of recognition as subspecies distinct from the typical one. The Sacramento Valley population is characterized by having broad, regularly arranged dorsal bands; the Santa Cruz Island population has narrow, irregular and angular bands, and seems to be of small size, but the number of specimens examined is insufficient to give a reliable indication of its characters. The Coronados Islands race, *nanus,* is distinguished mainly on the basis of its small size, reduced number of transverse ventral scale rows, and smooth scales. *G. m. webbii* of southwestern California and northwestern Lower California differs from the other races mainly in attaining larger size and having more heavily keeled scales.

The two Lower Californian species, *paucicarinatus* of the Cape Region, and *cedrosensis* of Cedros Island, are closely related to each other; in fact the degree of difference between them is about the same as that separating subspecies in other instances and it seems probable that they would intergrade if their ranges were not now separated by physiographic barriers. The *paucicarinatus-cedrosensis* stock is also closely related to the species *multi-carinatus* from which it differs mainly in slightly greater average numbers of dorsal scales (in both transverse and longitudinal series), in weaker and less extensive keeling of scales, and smaller size. *G. cedrosensis* differs from *paucicarinatus* in having fewer dorsal scales and in details of color pattern. *G. m. webbii,* the southernmost race of *multi-carinatus,* is the one geographically nearest to

paucicarinatus, but it is the farthest removed in structural characters (having numbers of scales reduced and carination increased). The geographically remote race *scincicauda* approaches *paucicarinatus* and *cedrosensis* most closely in characters.

Gerrhonotus kingii, of Arizona, New Mexico, and northwestern Mexico, is most closely related to *paucicarinatus* and *multi-carinatus,* but differs in having smoother scales, more transverse scale rows, shorter limbs, and a pattern of broader, more regularly arranged, transverse bands.

It seems probable that since the time when the range of the ancestral *paucicarinatus - multi-carinatus - kingii* stock became split into separate and isolated geographic entities, the wide-ranging species *multi-carinatus* has undergone more differentiation than the species *paucicarinatus* and *kingii* which are now restricted in range, and confined to high altitudes.

All members of the *coeruleus* group intergrade and hence are referred to the same species. In the past *coeruleus, principis* and *palmeri* have generally been regarded as distinct species, though it had been suggested that *coeruleus* and *principis* might intergrade. Lack of material from areas geographically intermediate between the ranges of the three forms made it impossible to demonstrate their relationships to each other. Before and during the course of the present study abundant material was amassed from these intermediate areas demonstrating the existence of a fourth form, *shastensis,* annectant between *principis, coeruleus,* and *palmeri.* With the series of *shastensis* now available it is possible to show gradual and complete geographic transition between these three, so that there can no longer be any doubt of their subspecific status. Indeed the completeness of intergradation in the material at hand renders it difficult to establish arbitrary lines of division between the respective ranges of the four well-defined form of *Gerrhonotus coeruleus.* The race *shastensis* of northern California and southwestern Oregon is large (compared with the other subspecies of *coeruleus),* has moderately keeled scales, relatively long legs, and peculiarities of color pattern (in which it is extremely variable,. Naturally it is intermediate in many of its characters since it is geographically situated between three other races and intergrades with all of them; however, it also has peculiar and distinctive characters which, along with its different *combinations of characters* set it off from the other races and seem to justify fully its recognition as a distinct race.

The wide-ranging subspecies, *principis,* occurring in British Columbia and Montana, west to the coast and south into the northwestern corner of California, is characterized by small size, retention of juvenal color pattern, weakly keeled scales, reduced number of longitudinal dorsal scale rows and short tail. *G. c .palmeri* of the Sierra Nevada has long legs, flattened body, heavily keeled scales, and dull, greenish ground color with markings reduced. Typical *coeruleus,* of the California coast from Sonoma County to Monterey County is the most specialized member of the group. It has small limbs, heavily keeled dorsal scales (of which the two mid-dorsal rows tend to become suppressed),

blunt and shortened muzzle with associated changes in numbers and shapes of scales, and peculiar color pattern.

Members of the *multi-carinatus* group are characteristic of warm, dry climates in austral life zones, while the species *coeruleus* is mainly confined to Transition and Boreal life zones in cooler and more humid climates. Differences in habits and structure between members of the two groups are evidently correlated with these habitat differences. Larger size is attained by the *multi-carinatus* group. Some members (and possibly all) of the *multi-carinatus* group are largely nocturnal in their foraging, (a tendency promoted by the warm climates in their ranges) and they have pale, unpigmented irises, but apparently *coeruleus* is strictly diurnal, and it has a dark heavily unpigmented iris. *G. multi-carinatus* is oviparous but *G. coeruleus* is viviparous; as in other northern or alpine reptile species, its viviparity is probably correlated with the unfavorable conditions for incubating eggs in the ground, occurring in the cold damp climate.

In the wide ranging species *multi-carinatus* and *coeruleus* those races which occur farthest north are markedly smaller than more southern races. Island populations which have undergone differentiation are usually dwarfed, at least such dwarfing is apparent in those of the Santa Cruz, San Miguel, San Martín and Coronados islands.

In both *multi-carinatus* and *coeruleus* those races which range farthest north have shortest tails, with fewest caudal whorls, and those forms which live in the warmest summer climates have longest tails; also in the mainly boreal species, *coeruleus*, the tail averages considerably shorter than in the austral *multi-carinatus*. This seeming correlation between tail length and climate may be comparable to instances, in many species of warm-blooded vertebrates, of progressive reduction in relative size of peripheral parts (ears, tail, bill, feet) in more northern populations as an adaptation to reduce loss of body heat. This parallelism may, however, be coincidental; varying size and shape of the tail might be more directly correlated with its utilization for various functions, as a reservoir for storage of fatty tissue or a prehensile organ for climbing.

Within both *coeruleus* and *multi-carinatus* the northern races tend to exceed the southern ones in numbers of transverse dorsal and ventral scale rows, but in *coeruleus* this tendency is slight. Apparently dwarfing is not correlated with reduction in numbers of scale rows, for small forms in several instances have more scale rows than larger ones. In both species there is a definite and progressive trend throughout their ranges toward greater extent and degree of carination of scales farther south. In each species the northernmost race is relatively smooth-scaled as compared with the southernmost.

General lack of parallelism in geographic trends of characters between *multi-carinatus* and *coeruleus* would seem to indicate that racial differentiation, if it is adaptive at all, is more responsive to ecological factors of the biotic environment than to those of climate affecting the general physical environment.

REFERENCES

BAIRD, S. F. 1858—Description of new genera and species of North American lizards in the museum of the Smithsonian Institution. Proc. Acad. Nat. Sci. Phila. **1857**:253-256.

———1859—Reptiles of the boundary. United States and Mexican Bound. Surv.: 1-35, 41 pls.

BAIRD, S. F. AND C. GIRARD. 1852—Description of new species of reptiles, collected by the U. S. Exploring Expedition under the command of Capt. Charles Wilkes, U. S. N. Proc. Acad. Nat. Sci. Phila. **6**:174-177.

———1853—Reptiles, *in* Exploration and survey of the valley of the Great Salt Lake of Utah, by H. Stansbury (Philadelphia, U. S. Senate doc., Appendix C): 336-365, pls. 1-7.

BEECHEY, F. W. 1831—Narrative of a voyage to the Pacific and Bering's Strait (Philadelphia, Cary and Lea), **2**: iv + 452 pp., 4 pls.

BLAINVILLE, M. H. D. DE. 1835.—Description de quelques espèces de reptiles de la Californie. Nouv. Ann. Mus. Nat. Hist. **4**: 1-64, pls. 24-27.

BOULENGER, G. A. 1885—Catalogue of the lizards in the British Museum, **2**: xiii + 497 pp., 24 pls.

COPE, E. D. 1875—Check-list of North American Batrachia and Reptilia. U. S. Nat. Mus. Bull. **1**:1-104.

———1883—Notes on the geographical distribution of Batrachia and Reptilia in western North America. Proc. Acad. Nat. Sci. Phila. **1883**:10-35.

———1900—The crocodilians, lizards and snakes of North America. Rept. U. S. Nat. Mus. **1898**:153-1270, 36 pls., 347 figs. in text.

DUMERIL, A. M. C. AND G. BIBRON. 1839—Erpétologie générale (Paris, Roret), viii + 854 pp.

FITCH, H. S. 1934a—New alligator lizards from the Pacific Coast. Copeia **1934**:6-7.

———1934b—A shift of specific names in the genus *Gerrhonotus*. Copeia **1934**: 172-173.

———1935—Natural history of the alligator lizards. Trans. Acad. Sci. St. Louis **29**:1-38, 4 pls.

GIRARD, C. 1858—Herpetology. U. S. exploring exped. (Philadelphia, J. B. Lippincott and Co.), **20**: xvii + 496 pp. and atlas, 3-10 pp., 32 pls.

GRAY, J. E. 1831—A synopsis of the species of the class Reptilia, *in* Griffith ed. of Cuvier, Animal kingdom (London: Whittaker, Treacher, and Co.), **9**: [appended] 1-110.

———1845—Catalogue of the specimens of lizards in the collection of the British Museum, 1-289 pp.

GRINNELL, J. AND C. L. CAMP. 1917—A distributional list of the amphibians and reptiles of California. Univ. Calif. Publ. Zool. **17**:127-208, 14 figs. in text.

GRINNELL, J., DIXON, J., AND J. M. LINSDALE. 1930—Vertebrate natural history of a section of northern California through the Lassen Peak region. Univ. Calif. Publ. Zool. **35**: v + 594 pp., 181 figs. in text.

McLAIN, R. B. 1899—Critical notes on a collection of reptiles from the western coast of the United States (Wheeling, West Va.), Contributions to North American herpetology: 13 pp.

O'SHAUGHNESSY, A. W. E. 1873—Herpetogical notes. Ann. and Mag. Nat. Hist. (4), **12**:44-48.

RIDGWAY, R. 1912—Color standards and color nomenclature, (Washington, D. C., published by the author), iii + 43 pp., 53 pls.

SCHMIDT, K. P. 1922—The amphibians and reptiles of Lower California and the neighboring islands. Bull. Amer. Mus. Nat. Hist. **46**:607-707, pls. 47-57.

SKILTON, A. J. 1849—Description of two reptiles from Oregon. Amer. Jour. Sci. Arts (2), **7**:202, 1 pl. [figs. 1-5].

STEJNEGER, L. 1893—Annotated list of the reptiles and batrachians collected by the Death Valley Expedition in 1891, with descriptions of new species. U. S. Dept. Agric. division ornithology and mammalogy, N. Amer. Fauna **7**:159-228.

———1902—*Gerrhonotus caeruleus* versus *Gerrhonotus burnettii*. Proc. Biol. Soc. Wash. **15**:37.

STEJNEGER, L. AND T. BARBOUR. 1917—A check list of North American amphibians and reptiles (Harvard University Press), iv + 5-125 pp.

STEPHENS, F. 1921—An annotated list of the amphibians and reptiles of San Diego County, California. Trans. San Diego Soc. Nat. Hist. **3**: 57-69.

VAN DENBURGH, J. 1896—Additional notes on the herpetology of Lower California. Proc. Calif. Acad. Sci. (2) **5**:1004-1008.

———1897—The reptiles of the Pacific Coast and Great Basin. Occas. Papers Calif. Acad. Sci. **5**:1-236.

———1898—The Gerrhonotus of the San Lucan Fauna, Lower California, with diagnosis of other west American species. Proc. Acad. Nat. Sci. Phila. **1898**: 63-66.

———1905—The reptiles and amphibians of the islands of the Pacific Coast of North America from the Farallons to Cape San Lucas and the Revilla Gigedos. Proc. Calif. Acad. Sci. (3), **4**:1-40, 8 pls.

———1912a—Notes on a collection of reptiles from southern California and Arizona. Proc. Calif. Acad. Sci. (4), **3**:147-154.

———1912b—Notes on some reptiles and amphibians from Oregon, Idaho, and Utah. Proc. Calif. Acad. Sci. (4), **3**:155-160.

———1922—The reptiles of western North America. Occas. Papers Calif. Acad. Sci. **10**:1-1028, 128 pls.

VAN DENBURGH, J. AND J. R. SLEVIN. 1914—Reptiles and amphibians of the islands of the west coast of North America. Proc. Calif. Acad. Sci. (4), **4**:129-152.

———1921—A list of the amphibians and reptiles of the peninsula of Lower California, with notes on the species in the collection of the Academy. Proc. Calif. Acad. Sci. (4), **9**:49-72.

WIEGMANN, A. F. 1828—Beiträge. Isis von Oken, **21**:364-383.

YARROW, H. C.—1883—Check list of North American Reptilia and Batrachia, with catalogue of specimens in U. S. National Museum. Bull. U. S. Nat. Mus. **24**:1-249.

YARROW, H. C. AND H. W. HENSHAW. 1878—Report upon the reptiles and batrachians collected during the years of 1875, 1876, and 1877, in California, Arizona, and Nevadaa. Rept. Chief U. S. Engineers *in* Ann. Rept. Sec. of War. **1878**: 1628-1648. Appendix NN.

The Biotic Districts of Oklahoma

W. F. Blair and T. H. Hubbell[1]

CONTENTS

INTRODUCTION ---- 425
BIOTIC DISTRICTS ---- 426
Ozark Biotic District ---- 427
Ouachita Biotic Districts ---- 428
Mississippi Biotic District ---- 430
Cherokee Prairie Biotic District ---- 431
Osage Savanna Biotic District ---- 433
Wichita Mountain Biotic District ---- 435
Mixed-grass Plains Biotic District ---- 437
Mesquite Plains Biotic District ---- 439
Short-grass Plains Biotic District ---- 440
Mesa de Maya Biotic District ---- 441
DISCUSSION ---- 442
The Orthoptera ---- 443
The Mammals ---- 448
SUMMARY ---- 451
REFERENCES ---- 454

Introduction

The study here presented is the outcome of investigations, begun independently by the two authors, of the distribution of the mammals and of the Orthoptera of Oklahoma. Each of us felt the need for definition and description of the major biotic areas of the state, to aid in interpreting the geographic and ecological distribution of the group with which he was concerned. Comparison of data indicated that the recognizable biotic units were the same for both groups of animals, and that they could be quite satisfactorily delimited. These conclusions were substantiated by further joint field work. Since it seems evident that these districts have significance for many groups of terrestrial animals, we feel that this study will be useful to other persons making distributional studies of the animals of this region.

This report is based primarily upon field studies by the authors. Hubbell worked in the Wichita Mountains in 1918 and 1930, spent the summer of 1926 making detailed studies of the Orthoptera of numerous localities in the western third of the state through the assistance of the Oklahoma Biological Survey, and in 1935 collected at several points in northern and eastern Oklahoma. Blair has conducted field studies, primarily of the mammals, in northern Oklahoma over a period of seven years. Both authors transected the state from its northeastern corner to the tip of the panhandle by automobile in the last week of August, 1937. Following this, Blair travelled by automobile from Tulsa south through the Osage Savanna to Antlers, thence across the Missis-

1 Contribution from the Museum of Zoölogy and Laboratory of Vertebrate Genetics, University of Michigan, and the Department of Biology, University of Florida.

sippi district and northward in extreme eastern Oklahoma and adjacent parts of Arkansas to Stilwell, and west to Tulsa. Notes on the vegetation and topography were made on the 1926 trip by Hubbell and other members of the Survey party, and plant collections were obtained at numerous points. Similar notes were kept on both 1937 trips, and plant collections and more complete notes were made at twenty-four stations. Blair also made some notes during an automobile trip in March, 1937, from Wyandotte in northeastern Oklahoma to Wichita Falls, Texas, and in May, 1937, from Amarillo, Texas to Tulsa. Thus the following account is based partly upon detailed studies made in localities representative of most of the districts, and partly upon extensive reconnaissance.

The discussion of the physiography of the various districts has been compiled largely from the accounts of Gould (1905), Snider (1917), and the Oklahoma Geological Survey (1930). The physiographic regions are those of Snider *(op. cit.)*. Climatological data have been taken from the U. S. Weather Bureau (1934). We are indebted to Paul C. Standley and O. W. Letson for the identification of many of the plants mentioned herein, and to L. R. Dice and C. L. Lundell for reading the manuscript. While numerous accounts by early travellers and exploring expeditions, as well as botanical and geological papers containing regional descriptions, have been consulted in the attempt to determine the boundaries and original conditions of the various districts, only papers cited are included in the bibliography.

Biotic Districts

An ecological association is considered here to include all of the plants and animals occurring together in a relatively stable environment. A biotic district is a geographic unit distinguished by the presence of unique ecological associations, or more often by the presence of a unique assemblage of widely distributed associations. It is less extensive than a biotic province, which generally is a major division of a continent, and usually several biotic districts are distinguishable within a province.

Ten biotic districts are distinguished in the state of Oklahoma. Most of the districts extend beyond the limits of the state, but here only the parts of the districts lying in Oklahoma are considered. In the following pages the physiographic, climatic, and floristic characteristics of the biotic districts in Oklahoma are discussed. The orthopteran and mammalian constituents of these districts are treated only briefly, since their distribution in the districts will be taken up later in detail in separate papers.

Ozark Biotic District

Location: The Ozark biotic district coincides with the Ozark highland in northeastern Oklahoma, and extends east into Arkansas and Missouri. It is characterized by the presence of the Boone chert, and its western boundary is formed by the Grand River, which flows along the western outcrop of the formation.

Physiography and geology: The Oklahoma part of the district is drained by the Grand and Illinois rivers. The tributaries of these streams are clear and cold, since they are largely spring-fed. The region is a rather deeply dissected plateau. The Boone chert, which is a formation of alternating limestone and flint layers, has been eroded to form the hills, incised valleys, and prominent bluffs that produce the rugged topography characteristic of the Ozark biotic district. The chert has weathered into sharp, angular fragments which form a mantle sometimes as much as twenty or thirty feet deep on the slopes. Much of the drainage of the region is under-ground, and there is an abundance of sinks and caves. The greatest elevation in the region is about 1,500 feet in eastern Adair County. The maximum elevation of the hills above their bases is about 400 feet.

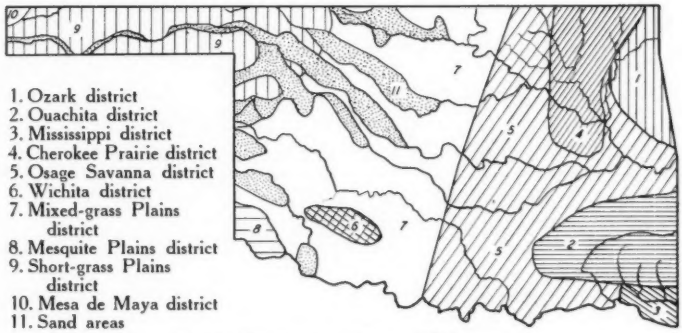

Fig. 1. The Biotic districts of Oklahoma.

Climate: The average annual temperature at Tahlequah, Cherokee County, is 60.1° F. (30 year record), and the average annual rainfall is 42.38 inches. The average length of the growing season is 209 days.

Principal plant associations: The most widely distributed plant association of the Ozark biotic district is the dry, oak-hickory forest that covers the chert-mantled hillslopes and crests. The principal trees are blackjack oak *(Quercus marilandica)*, post oak *(Quercus stellata)*, black hickory *(Carya buckleyi)*, and winged elm *(Ulmus alata)*. The ground cover is sparse and is formed principally by low huckleberries and by coral berry *(Symphoricarpos orbiculatus)*. Sassafras *(Sassafras variifolium)* is a prominent shrub.

Slopes with seepage zones, steep north-facing slopes, and protected ravines support a more mesic plant cover. Typical trees are sugar maple *(Acer saccharum)* and hop hornbeam *(Ostrya virginiana)*, while others, including white oak and chinquapin oak *(Quercus alba* and *Q. muhlenbergii)*, redbud *(Cercis canadensis)*, flowering dogwood *(Cornus florida)*, and linden *(Tilia* sp.) are also important. The chief shrubs are spice bush *(Benzoin aestivale)*, hazelnut

(Corylus sp.), wild hydrangea *(Hydrangea arborescens),* papaw *(Asimina triloba),* bladder nut *(Staphylea trifolia),* sassafras, and coral berry. The forest floor is generally blanketed by an abundance of herbaceous mesophytes, of with bloodroot *(Sanguinaria canadensis),* wild ginger *(Asarum canadense),* yellow dogtooth violet *(Erythronium americanum),* may apple *Podophyllum peltatum)* and maidenhair fern *(Adiantum pedatum)* are representative. Mosses, ferns, and liverworts are abundant in many places.

Exposed limestone and chert bluffs generally bear a more or less dense cover of juniper *(Juniperus virginiana),* in which occur such other trees as blackjack oak and winged elm. These bluffs are almost devoid of soil, and most of the plants grow from crevices in the rocks. The sparse, herbaceous cover is largely composed of saxicolous species, of which the purple cliff brake *(Pellaea atropurpurea)* and columbine *(Aquilegia canadensis)* are representative.

The larger stream valleys have open, rather barren forests on their floodplains. Characteristic trees are silver maple *(Acer saccharinum),* red birch *(Betula nigra),* American elm *(Ulmus americana),* cottonwood *(Populus deltoides),* sycamore *(Platanus occidentalis),* linden, and various oaks. The forest floor may be sandy or covered with humus and supporting a good cover of grass, or it may be made up of water-worn chert pebbles, with no herbs or grasses. Lizard's tail *(Saururus cernuus)* is a characteristic herb near water. There is a fringe of Ward's willow *(Salix longipes* var. *wardii)* along the margins of the streams.

Cleared fields and treeless areas on the level upland are occupied by weeds and grasses and are being invaded by persimmon *(Diospyros virginiana),* sassafras, coral berry, and honey locust *(Gleditsia triacanthos).* Ortenburger (1928b, 57) listed among other herbs, dog fennel *(Anthemis cotula),* horse mint *(Monarda mollis),* skullcap *(Scutellaria cordifolia),* and ironwood *(Vernonia baldwinii)* from a station near the Illinois River.

The forest types of this biotic district were described by Turner (1935), and Steyermark (1934) discussed the relationship between the herbaceous plants and the types of subsoil.

Ouachita Biotic District

Location: This biotic district corresponds to the Oklahoma part of the Ouachita Mountains, and extends with the mountains into southern Arkansas.

Physiography and geology: This is the roughest, most mountainous part of Oklahoma. It is a region of high, even-crested sandstone ridges and broad, flat, east-west-trending valleys. From the Arkansas border (where Rich Mountain attains an elevation of 2,850 feet above sea-level, and the maximum height of the ridges above the valleys is about 1,800 feet) the summit levels decline westward to the termination of the mountains near Atoka (where the crests are about 750 feet above sea-level and about 250 feet above the valleys). To the south a narrow and interrupted Piedmont belt fronts the Mississippi district, while to the north and west the Ouachita district merges less abruptly into the Arkansas valley portion of the Osage Savanna.

The slopes generally have thin soils and are littered with boulders. There are local areas of flint hills. The principal valleys have developed on less resistant beds of shales and slates. The drainage of the southern part of the mountains flows into the Red River by way of Little River, while that of the northern part is carried to the Arkansas by Poteau River. The tributaries of these streams are clear and swift.

Climate: The climate on the whole is mild, free from extreme cold in winter, but at times intensely hot in summer. The average annual temperature at Antlers in the southwestern part of the district is 63.2° F. (13 year record), while at Poteau near the northern boundary it is 62.9° F. (14 year record). The maximum rainfall occurs in the spring or early summer, the minimum in late summer or fall. The average annual rainfall at Antlers is 51.73 inches, at Poteau 42.09 inches. The average length of the growing season at Antlers is 229 days, at Poteau 216 days.

Principal plant associations: The most extensive plant association of the Ouachita biotic district is an open forest of yellow pine *(Pinus echinata)*, mixed with oaks and other trees. Of these latter, Palmer (1924, 113) listed white oak *(Quercus alba)*, post oak *(Quercus stellata)*, blackjack oak *(Quercus marilandica)*, mocker-nut hickory *(Carya alba)*, Arkansas hickory *(Carya buckleyi* var. *arkansana)*, and black locust *(Robinia pseudoacacia)*, as associates of the shortleaf pine on the slopes of Rich Mountain. According to the same author huckleberries form most of the shrub cover, and the most common species is *Vaccinium vacillans* var. *crinitum*. Much of this forest is in virgin condition or nearly so.

Protected ravines and north-facing slopes have mesic forests that differ from those in similar situations in the Ozark district chiefly in that they have a number of plants that are rare or absent in the Ozarks. Little and Olmstead (1936, 54) listed white oak as the dominant tree in such situations, and linden *(Tilia floridana)*, mocker-nut hickory, sugar maple *(Acer saccharum)*, and spotted oak *(Quercus shumardii)*, as characteristic species. Red maple *(Acer rubrum)* is abundant in these mesic situations, and to the list should be added some of the species listed by Palmer (1924, 114-134) from the vicinity of Rich Mountain, including cucumber tree *(Magnolia acuminata)*, southern witchhazel *(Hamamelis macrophylla)*, sweetgum *(Liquidambar styraciflua)*, and a holly *(Ilex caroliniana)*. Characteristic shrubs and herbs *(ibid.)* are Christmas fern, maidenhair fern, marginal shield fern, mockorange *(Philadelphus pubescens)*, strawberry bush *(Evonymus americanus)*, pink azalea *(Rhododendron roseum)*, gooseberry *(Ribes cynosbati)*, papaw *(Asimina triloba)*, spice bush *(Benzoin aestivale)*, bladder nut *(Staphylea trifolia)*, and silverbell *(Halesia monticola* var. *vestita)*. The herbs are mesophytes that belong for the most part to the same species that occur in similar situations in the Ozark biotic district.

The mountain streams are generally choked with sandstone blocks and are fringed by such shrubs as those listed by Palmer *(op. cit.*, 110), including kinnikinnik *(Cornus obliqua)*, Ward's willow *(Salix longipes* var. *wardii)*, buttonbush *(Cephalanthus occidentalis)*, alder *(Alnus rugosa)*, and French

mulberry *(Callicarpa americana)*. Boggy areas along these streams have a heavy cover of herbs and ferns. The flood-plains of the larger streams have a heavy forest of white oak, post oak, black oak *(Quercus velutina)*, sweetgum, tupelo *(Nyssa sylvatica)*, linden, mocker-nut and Arkansas hickory, sugar maple, and yellow pine. Among the shrubs are spice bush, sassafras, and papaw. Water oak *(Quercus nigra)* and willow oak *(Quercus phellos)* grow along the borders of the streams.

Palmer *(op. cit.,* 117) described a dwarfed forest on the summit of Rich Mountain that probably occurs also on others of the higher peaks. The trees are seldom more than thirty feet tall, and their branches are gnarled and twisted. The most common trees are blackjack, black and post oaks, mockernut and Arkansas hickories *(Castanea ozarkensis)*, sassafras, and persimmon. Where the mountain top is more rocky there are thickets formed by several species of plums, fringe tree *(Chionanthus virginica)*, witchhazel, blackberries, a buckeye *(Aesculus glabra* var. *monticola)*, dwarf sumac *(Rhus copallina)*, and others.

Prairie openings are less numerous and less extensive than in the Ozark district. Such openings on the side and crest of Blackfork Mountain were found by Palmer *(op. cit.,* 113) to have bluestem *(Andropogon* sp.), dropseed *(Sporobolus* sp.), Indiangrass *(Sorghastrum* sp.), low huckleberries, St. Andrew's cross *(Ascyrum hypericoides)*, and various species of *Aster, Solidago,* and *Lespedeza.*

Mississippi Biotic District

Location: This district is limited in Oklahoma to the part of the Gulf coastal plain occupying the southern half of McCurtain County in the southeastern corner of the state. The area in Oklahoma is only a small part of the district, which extends southeastward on the coastal plain in southern Arkansas, Louisiana, and easternmost Texas. Northward the district is sharply bounded in Oklahoma by the Ouachita district, but on the west, in the Red River valley, it passes gradually into the Osage Savanna district.

Physiography and geology: This is a relatively featureless plain, somewhat rolling where it approaches the Ouachitas, and lying mostly between 300 and 500 feet above sea-level. It is formed of nearly level Cretaceous sands and clays deposited on the truncated edges of the southward-dipping, older rocks of the Ouachita Mountains. A belt varying from 12 miles in width at the Arkansas line to less than two miles at the western edge of the district is overlain by Quaternary flood-plain and terrace deposits of the Red River, and this portion exhibits most typically the biotic features characteristic of the district. In contrast with the clear, swift, trellis-pattern streams of the Ouachita district, those of the Mississippi district are sluggish, south-flowing consequent streams tributary to Little River and the Red River. They occupy shallow valleys or mere channels in the level flood-plain, and are generally mud-banked.

Climate: This is the warmest and most humid part of the state. The aver-

age annual temperature at Idabel is 65.6° F. (14 year record), and the average annual rainfall is 45.40 inches. The average length of the growing season is 240 days.

Principal plant associations: The Mississippi biotic district brings into Oklahoma a number of forest types that are unique for the state, but which are widely distributed southeastward on the Gulf coastal plain. Extensive cypress swamps, in which bald cypress *(Taxodium distichum)* is the dominant tree, occur along Little River and appear to be identical in character with similar swamps farther south. Sweetgum *(Liquidambar styraciflua)* is one of the most important trees of the district. It grows with tupelo *(Nyssa sylvatica)* and water oak *(Quercus nigra)* on moist flood-plains (Little and Olmstead, 1936, 54). On cut-over land it is also mixed with pines, which were identified by Little and Olmstead *(op. cit.,* 55) as *Pinus taeda* and *P. echinata,* to form one of the most extensive associations of the district. The young sweetgums form a dense cover of thicket-like aspect, interrupted by open areas shaded by mature pines. On the rich soil of river terraces the sweetgums are mixed with white oak *(Quercus alba),* red maple *(Acer rubrum),* and American holly *(Ilex opaca)* to form a dense, well-shaded forest. Characteristic shrubs are French mulberry *(Callicarpa americana),* papaw *(Asimina triloba),* and Hercules'-club *(Zanthoxylum clava-herculis),* although numerous others are also present. The palmetto *(Sabal glabra)* was recorded from low, wet, wooded areas by Clark (1935, 38). There are many lianas. The forest floor has a rather heavy accumulation of leaf-mold, and there are many ferns and shade-tolerant herbs.

Cherokee Prairie Biotic District

Location: The Cherokee Prairie biotic district lies west of the Ozark district, and is bounded on the west and south by the Osage Savanna district. It is continuous with the prairies of eastern Kansas and of the states to the east.

Physiography and geology: This district coincides generally with the Prairie Plains physiographic region. The surface is fairly even and slopes to the south and east. The elevation above sea-level averages about 700 feet. There are east-facing limestone and sandstone escarpments with gentle slopes to the west, separated by broad valleys underlain by shale. The area is drained by the Verdigris River and by tributaries of the Grand River. The streams are sluggish and muddy and are generally intrenched in broad flood-plains.

Climate: The average annual temperature in the area is about 60° F. The average annual rainfall varies from 43.15 inches (35 year record) at Vinita in the northern part of the area to 37.40 inches (47 year record) at Tulsa, at the western border of the district. The average length of the growing season is 200 days (29 year record) at Vinita, and 218 days (25 year record) at Tulsa.

Principal plant associations: The ecological associations of the Cherokee Prairie district have been described by Blair (unpublished manuscript). Tallgrass sod on shale soils is the most extensive plant association. This sod is

produced by bluejoint *(Andropogon furcatus)*, prairie beardgrass *(Andropogon scoparius)*, Indiangrass *(Sorghastrum nutans)*, and switchgrass *(Panicum virgatum)*. Typical herbs are false indigo *(Baptisia bracteata)*, blazing stars *Liatris punctata* and *(L. scariosa)*, starwort *(Aster multiflorus)*, sunflower *(Helianthus mollis)*, and sage *(Salvia azurea* var. *grandiflora)*. Where the original, heavy sod has been destroyed (as has occurred over extensive areas) there is a sparse cover of crab-grass *(Digitaria sanguinalis)*, windmill grass *(Chloris verticillata)*, other grasses, and weeds, including kindling weed *(Amphiachyris dracunculoides)*, croton *(Croton capitatus)*, and others.

On the thin soil of limestone scarps, there is a dry prairie characterized by the intermixture of tall and short grasses. The principal grasses of this association are side-oats grama *(Bouteloua curtipendula)*, buffalo-grass *(Buchloë dactyloides)*, and silver beardgrass *(Andropogon saccharoides)*. Other plants representative of the dry prairie are the blue false indigo *(Baptisia australis)*, stone-crop *(Sedum pulchellum)*, gaillardia *(Gaillardia pulchella)*, prickly pear *(Opuntia humifusa* and *O. tortispina)*, and yucca *(Yucca glauca)*. The ground cover is interrupted over most of the limestone prairie by exposed limestone slabs and gravels. Small persimmon *(Diospyros virginiana)* trees and shrubs occur on the limestone prairie in open groves, or they may be widely scattered. Shallow, prairie drains often have persimmons on their slopes and indigo plants *(Amorpha fruticosa)* along the margins of the watercourses. As the drains become larger and are bordered by flood-plains, they are lined by an open stand of American elm *(Ulmus americana)*, hawthorn *(Crataegus* sp.), woolly buckthorn *(Bumelia lanuginosa)*, and other trees.

Sheltered ravines are occupied by many plants characteristic of the moist ravines of the Ozark district, mixed with spotted oak *(Quercus shumardii)*, chinquapin *(Quercus muhlenbergii)*, and other trees which predominate in the dryer ravines. Limited areas of dry oak-hickory forest occur on the level limestone outcrops. The dominant trees of this association are blackjack oak *(Quercus marilandica)*, post oak *(Quercus stellata)*, and black hickory *(Carya buckleyi)*. There is a considerable cover of herbs, which are principally prairie species, and the typical grasses of the dry prairie occur in unshaded parts of this association. Abundant shrubs are smooth sumac *(Rhus glabra)* and coral berry *(Symphoricarpos orbiculatus)*, which extend beyond the limits of the oak-hickory forest to form thickets with shrubby persimmons and prairie grasses and herbs. Travertine is being formed in the ravines having fairly permanent streams. Another feature of these ravines is the rim-rock or limestone outcrop that caps their slopes.

The broader flood-plains are covered by a mature forest in which American elm, slippery elm *(Ulmus fulva)*, spotted oak, pin oak *(Quercus palustris)*, and hackberries *(Celtis occidentalis* and *C. laevigata)* predominate. The forest floor is well-shaded and generally has an accumulation of leaf-mold. Most of the forest has been cut over, so that it is now composed of scattered mature trees, alternating with younger trees and thickets or weedy areas. The chief shrubs are burning bush *(Evonymus atropurpureus)*, prickly ash *(Zan-*

thoxylum americanum), American elder *(Sambucus canadensis)*, and smooth and dwarf sumac *(Rhus glabra* and *R. copallina)*. Heavy, grassy cover is formed in unshaded areas by bluejoint, broadleaf uniola *(Uniola latifolia)*, switchgrass, and Virginia wild rye *(Elymus virginicus)*. With these are mixed such other herbs as cone-flowers *(Rudbeckia triloba* and *R. subtomentosa)*, Joe-pye weed *(Eupatorium purpureum)*, ironweed *(Vernonia altissima)*, and others.

Poorly drained parts of the flood-plains are generally occupied by buttonbush *(Cephalanthus occidentalis)* or sedges *(Carex* sp.), or the two may be intermingled to form dense thickets with occasional patches of sedge marsh. This association is more or less flooded during the winter and spring and is usually dry in summer. Flood-plain lakes are surrounded by willows (generally *Salix nigra)*, buttonbush, and green ash *(Fraxinus pennsylvanica* var. *lenceolata)*. They may support an abundance of aquatic plants, including cat-tail *(Typha latifolia)*, American lotus *(Nelumbo lutea)*, and others. The permanent streams are bordered by black willow *(Salix nigra)*, cottonwood *(Populus deltoides)*, sycamore *(Platanus occidentalis)*, and silver maple *(Acer saccharinum)*. There are extensive mud flats along some of the larger streams.

Osage Savanna Biotic District

Location: The Osage Savanna biotic district occupies all of Oklahoma east of a line running north from eastern Jefferson County to north-central Osage County, excepting the Ozark, Ouachita, Mississippi, and Cherokee Prairie districts. It is continuous with the Cross-timbers of Texas, and extends northward a short distance into Kansas.

Physiography and geology: The Osage Savanna district includes all of the Sandstone Hills, Lower Arkansas Valley, and Arbuckle Mountains physiographic regions. The southern tip of the Prairie Plains region and a large part of the Red River region are also included. The surface of most of the district is rough, due to the differential weathering of alternate layers of shales and resistant sandstones, but rolling plains and alluvial flats occur in the valleys of the larger streams. The sandstones have weathered into ledges and form pronounced escarpments and hills, the slopes and tops of which are covered with large sandstone blocks. The greatest elevation is attained by isolated peaks in the lower Arkansas valley region, which rise to 1,500 feet above sea level. The streams which rise in the district are generally clear, but are not so cold as those of the Ozarks.

Climate: The average annual temperature varies from 63.5° F. in the south (average of 28 to 33 year records at Ada, McAlester, Ardmore, and Durant) to 59.3° F. in the northern part of the state (32 year record at Pawhuska). As a rule the winters are short, with extremely cold weather rare, the summers long and with occasional periods of very hot weather. The average length of the growing season varies from 205 days in the north to 235 days in the south. The average annual rainfall is about 38 inches throughout most of the region

(42.5 at McAlester in the lower Arkansas valley over a 29 year period), and shows a slight decrease westward.

Principal plant associations: The sandstone hills and escarpments are covered by a dry, scrubby forest mostly composed of blackjack oak *(Quercus marilandica)*, post oak *(Quercus stellata)*, and black hickory *(Carya buckleyi)*. There are many second-growth sprouts of the two oaks, with which are often mixed dwarf sumac *(Rhus copallina)* and coral berry *(Symphoricarpos orbiculatus)*. The bluejoint *(Andropogon furcatus)* has the bunch-grass type of growth in this association, and some other herbs are present. However, the general aspect of the forest floor is one of sandy soil with a sparse cover of grasses and other herbs, and littered in places with sandstone blocks of varying sizes.

Protected or north-facing sandstone bluffs have a more mesic type of vegetation, with spotted oak *(Quercus shumardii)* generally dominant. Redbud *(Cercis canadensis)*, juneberry *(Amelanchier canadensis)*, and winged elm *(Ulmus alata)* also characterize this association. Grasses are broadleaf uniola *(Uniola latifolia)* ,Virginia wild rye *(Elymus virginicus)*, Japanese chess *(Bromus japonicus)*, and others. There are many herbaceous mesophytes. On well-shaded slopes mosses, liverworts, and fruticose lichens form a continuous mat over the surface of the ground.

The streams, near their headwaters in the hills, are choked with sandstone and limestone blocks, so that pools remain in many places even in drought years. Many of the streams are filled with aquatic mosses. Red birch *(Betula nigra)*, black willow *(Salix nigra)*, and buttonbush *(Cephalanthus occidentalis)* grow in the beds of these small streams, and as the streams become wider and develop flood-plains the same species grow along the stream banks. The flood-plain forest is more mesic than the forest of the surrounding hills and is comparable to the flood-plain forest of the Cherokee Prairie district.

The level or rolling areas on shale soils have grassland communities somewhat similar to those on the limestone scarps in the Cherokee Prairie district. This type of grassland is most closely related to the grasslands of the Mixed-grass Plains district, and it affords a highway for the eastward extension of western species of animals. Much of the grassland of the Osage Savanna district has suffered from over-grazing to such an extent that few of the native grasses are left. They have been replaced by a sparse cover of weeds that has an extremely barren aspect, especially in dry years. Groves of shrubby persimmons *(Diospyros virginiana)* occur on the grassland in some places. The relative amount of grassland and forest varies greatly in different parts of the district. In the more sharply dissected areas there is little or no grassland, while in the more level areas the grassland predominates, and the forest is restricted to occasional ravines.

The Arbuckle Mountains, here included in the Osage Savanna district, possess certain distinctive features which require mention. While the dissected limestone plateau that forms the mountains has an area of between 600

and 800 square miles and extends nearly 50 miles from east to west, only that part west of the Washita River and lying mostly in Murray County is sufficiently elevated to be termed mountainous. Near the western edge the summits reach an elevation of about 1,300 feet above sea level, and stand some 400 feet above the surrounding country. In this higher part of the Arbuckle Mountains, hard limestone strata form east-west-trending ridges along the northern and southern margins of the central plateau, with broad intervening valleys cut in the softer shales and sandstones. The Washita River flows in a deep gorge across the uplift, and smaller streams such as Fall Creek and Honey Creek have cut narrow, rock-walled valleys in which occur numerous water-falls due to travertine deposits. There are many large springs and limestone caves. Although the plant associations of the region are for the most part the same as those of the rest of the Osage Savanna district, the more extensive development of mesic ravine forests, the abundance of rock ledges, the presence of the caves, and the prevailingly calcareous streams and soils give this area a somewhat different aspect.

Wichita Mountain Biotic District

Location: The Wichita Mountains consists of several low ridges and groups of hills, extending from Fort Sill in Comanche County northwestward to just beyond Granite in Greer County, a distance of 65 miles. From Fort Sill the northern and southern limits of this peculiar collection of mountains diverge until, near the center, the outlying knobs upon each side are 30 miles apart. Continuing northwestward the range gradually contracts and ends near Granite in small collections of low mountains or knobs. The group is entirely surrounded by the Mixed-grass Plains district.

Physiography and geology: The mountains are the summits of buried monadnocks, protruding through the level Redbeds Plains that surround them. For the most part they are composed of granite and gabbro, but a range of limestone hills lies along the northeastern side of the group, and parts of the main mountain mass are Cambrian sandstone. The topographic expression of the various rocks does not differ markedly. Many of the outliers (ranging in size from mere hillocks to mountains covering several square miles) stand isolated in the plain, rising abruptly to heights as much as 400 or 600 feet above it. The main mountain group occupies an area of more than 200 square miles (18 by 8-12 miles). A number of the higher peaks of this group exceed 2,400 feet in elevation above sea-level, and rise about 1,000 feet above the plains. The lower hills and slopes are covered with a thin mantle of residual soil, but the upper slopes of the higher peaks are steep and rugged, strewn with often immense talus boulders, and frequently almost barren of soil. There are a few caves.

The region is drained by numerous small streams, flowing for the most part southward into the Red River. Many of these are dry except after rains, or in periods of drought are reduced to occasional pools; but others which head in the mountains are spring-fed and permanent, with clear, cool water. Most

of the streams which penetrate or traverse the district flow in broad, level-floored intermontane valleys occupied by embayments of the Redbeds, in which the streams have cut shallow channels. In a number of instances the streams have been superposed on the buried ranges, and now flow through them in narrow, steep-walled, rocky gorges as much as 200 feet deep. Otter, West Cache, Panther, and Beaver creeks have cut such canyons. Two of the streams in the eastern part of the mountains have been dammed to form artificial lakes, one of which is of considerable size.

Climate: The climate is essentially that of the southern part of the Mixed-grass Plains district. The average annual temperature at Lawton (just east of the mountains) is 62.0° F. (34 year record), the average annual rainfall is 31.53 inches, and the average length of the growing season is 219 days (19 year record).

Principal plant associations: The Wichita Mountains are surrounded and permeated by the Mixed-grass Plains biota. Toward the peripheries of the district the plains predominate, interrupted only by occasional hills and ridges. Some of these isolated hills are grass-covered and scarcely differ from the plains, but others have barren, rocky slopes and summits, and support little or no vegetation.

In the main Wichita group the mountains are higher and more continuous, restricting the grassland to the level valley floors and flat summits of some of the lower hills. The grassland shows marked response to the various edaphic conditions present. The lower and moister parts of the valley floors, where protected from over-grazing and not forested, have a dense sod-forming growth of tall grasses and associated herbs suggestive of the tall-grass sod of the Cherokee Prairie district. On the more xeric hilltops and on the over-grazed lowlands the grasses are low, sparse, and tufted, interspersed with occasional clumps of *Opuntia,* and specifically identical with those of the drier parts of the Mixed-grass Plains district. The biota of the grassland parts of the Wichita Mountain district is that of the surrounding plains, and these grassland associations occupy at least two-thirds of the area of the district. An occasional clump of mesquite is representative of an attenuated western element in the biota of these plains.

A mesophytic forest borders the streams of the more enclosed valleys, composed principally of spotted oak *(Quercus shumardii),* hackberry *(Celtis laevigata* var. *texana),* black walnut *(Juglans nigra),* American elm *(Ulmus americana),* woolly buckthorn *(Bumelia lanuginosa),* and white ash *(Fraxinus americana),* with other trees, some of them of eastern affinities. This forest is best developed in the ravines and canyons, the trees in such protected sites being larger and forming a denser canopy, and the proportion of eastern plant species being greater. The ravine forests resemble those described under the Mixed-grass Plains district, but are more extensively developed in the Wichitas. Such endemism as is encountered among the animals of this district is attributable in part to the isolation of this moderately large expanse of mesophytic forest.

The lower granite hills and the south-facing slopes of the higher mountains are covered with a scrubby, xeric forest composed mostly of blackjack oak *(Quercus marilandica)* and post oak *(Quercus stellata)*. The tree growth is open, with numerous glades, and with tufted grasses growing in soil-filled crevices and among the talus boulders. On north-facing slopes the forest is denser and somewhat less xeric, and there are occasional patches of dense shrubbery and tangles of vines. In places the blackjack forest spreads away from the mountain base and merges with the mesophytic forest of the stream-borders; elsewhere it thins out and gives place to grassland. This dry oak forest is the most extensive plant association of the Wichita Mountains proper. It closely resembles the xeric forests of the sandstone ridges of the Osage Savanna district.

The summits of the highest peaks of the district are treeless, except for scrubby junipers and an occasional stunted oak. Some of them are weathered masses of granite, almost without vegetation; others have scanty growths of bunch-grasses, artemisia, and various saxicolous herbs in the interstices between the talus boulders. The bare rock and lichen-covered cliffs and ledges form an extensive habitat type in which a few characteristic endemic animals are found. A few small springs and seepage areas on the upper slopes are bordered with grasses and herbage.

Mixed-grass Plains Biotic District

Location: This district is bounded on the east by the western limits of the Osage Savanna district, and, exclusive of the Panhandle, it comprises all of western Oklahoma except the Wichita Mountains, a small area in the southwest, and one in the northwest. It extends northward through Kansas and southward into Texas.

Physiography and geology: This district includes both the Redbeds Plains and Gypsum Hills physiographic regions. The surface slopes to the southeast, and the elevation varies from about 1,500 feet in the northwest to less than 1,000 feet in the southeast. The district is a slightly rolling plain, into which the streams have cut shallow channels separated by broad, flat-topped interstream areas. In the Gypsum Hills region the topography is more rugged owing to the presence of gypsum ledges, and in this section some streams have cut narrow channels that are in places 200 to 400 feet deep. The rocks are mostly Permian Redbeds—soft red shales and red sandstones, decomposition of which has produced the extremely red soils characteristic of most of the district. The drainage is mostly eastward into the Arkansas River system, but the southern part of the area drains into the Red River. In the gypsum strata of the western part of the district there are extensive caves.

Climate: The average annual temperature varies from 62.7° F. (18 year record) at Altus in the southwestern part of the district to 58.6° F. (31 year record) at Alva near its northwestern border. The average annual rainfall deceases westward from 31.59 inches (40 year record) at Oklahoma City to 26.79 inches (17 year record) at Altus, and 28.71 inches (24 year record) at

Alva. The length of the growing season varies from 224 days (17 year record) at Altus in the south to 203 days (30 year record) at Alva in the north.

Principal plant associations: This biotic district includes the Oklahoma sections of the *Stipa-Koeleria* and *Stipa-Bouteloua* associations of Clements (1920, 121, 135) and of Bruner (1931, 167, 175). The district is essentially an area of transition from the tall-grass prairies of the east to the short-grass plains of the west, and forms a well-marked biotic district of considerable importance. Despite its division into two phytogeographic areas this district is relatively uniform from east to west, although there is some decrease in the amount of cover with increasing aridity westward. The district is characterized by the mixture of tall grasses from the east and short grasses of western affinities. The chief dominants of the two divisions of Bruner *(loc cit.)* as listed by him are essentially the same, and *Stipa* and *Koeleria,* from which the eastern division derives its name, are admitted by him to be scarce and of little importance in Oklahoma.

The most extensive plant association of the district is the grassland that covers the level or rolling plains of most of the area. It is sod-forming in local areas of favorable soil and moisture conditions, as noted in the discussion of the Wichita Mountain district, while in more xeric situation the grassland may be open with the grasses occurring in bunches. In moist years the grasses form a heavy ground cover, although it is not comparable to that of the tall-grass prairie. In dry years the ground cover is sparse in all except the most mesic situations. The important grasses of this association listed by Bruner *(loc cit.)* are prairie beardgrass *(Andropogon scoparius),* silver beardgrass *(Andropogon saccharoides),* bluejoint *(Andropogon furcatus),* bluestem *(Agropyron smithii),* and such short grasses as buffalo-grass *(Buchloë dactyloides),* and several species of grama grasses *(Bouteloua gracilis, B. racemosa,* and *B. hirsuta).* Side-oats grama *(Bouteloua curtipendula)* is also important. On the thin soil of gypsum scarps in the western part of the district short grasses prevail to form local islands of grass similar to the grasslands of the Short-grass Plains district.

An important association of the Mixed-grass Plains district is that existing on sand dunes and the sandy areas along the northern sides of most of the large streams, because these sandy areas are highways for the eastward extension of many western species of animals, in addition to having a distinctive fauna of their own. Numerous variations in plant cover, from the conditions on live dunes devoid of plants to those on stable sand with thickets of woody plants, exist in this area. However, there are numerous plants characteristic of the association, and the local variations are due largely to the relative abundance of these plants. Bluejoint is the principal grass, and here it is entirely a bunch grass. Yellow-haired beardgrass *(Andropogon chrysocomus)* was listed by Bruner *(op. cit.,* 160) as one of the dominants in this association. Sand sage *(Artemisia filifolia)* is the most characteristic plant of the sand areas and usually forms a major part of the ground cover. In many places there are dense thickets formed by Chickasaw plum *(Prunus angustifolia)*

and stinking sumac *(Rhus trilobata)*. These shrubs seldom exceed 5 feet in height, and they are often less. Sand sage and bunch grasses occur also in these thickets. In the southwestern part of the district the sandy areas are mostly covered by a dense stand of shin-oak *(Quercus havardii* according to Shantz, 1923, 103), which is generally less than two feet in height. Bruner (1931, 155) mentioned *Quercus mohriana, Q. stellata palmeri, Q. s. rufescens,* and *Q. vaseyana* as constituents of the shin-oak. The salt plains of various localities in the northern part of the district constitute a variation of the sand areas in which there is an attenuation of the biota, with the introduction of a small number of animals confined to this habitat type.

The cottonwood *(Populus deltoides)* occurs along the margins of the streams. In many places the sandy flats along the streams are occupied by an open stand of tamarix shrubs *(Tamarix gallica,* according to Hefley, 1937, 358). Locally there are small stands of mesquite on the river terraces. The oak-elm forest of the eastern stream valleys extends out into this district for varying distances along the streams. In the eastern part of the district this forest is not appreciably different from the more eastern stream valley forests, but westward it becomes more and more dry and limited in extent until most of it disappears before the western limits of the district are reached. These forests are highways for the westward extension of eastern forest species of animals.

Narrow, steep-walled ravines in the western and central parts of this district often support isolated patches of forest made up of eastern species of trees. In such situations the steep, rocky slopes of the ravines generally have a good cover of oaks *(Quercus shumardii* and *Q. muhlenbergii)* mixed with junipers. On the ravine floors the oaks are mixed with American elm *(Ulmus americana),* black walnut *(Juglans nigra),* and other deciduous trees to form a well-shaded forest. Such a ravine in Caddo County was found by Little (1936, 47) to have a tall forest of about 20 species of deciduous trees, of which sugar maple *(Acer saccharum),* black walnut, chinquapin oak, spotted oak, hackberry *(Celtis laevigata),* and boxelder *(Acer negundo)* are representative. The ravine also has a number of mosses, ferns, and flowering herbs with eastern affinities.

Mesquite Plains Biotic District

Location: The part of the Mesquite Plains biotic district occurring in Oklahoma is limited to the extreme southwestern corner of the state, in southern Harmon and Jackson counties. This district extends southwestward through an extensive area in Texas. Its boundaries in Oklahoma are less sharply defined than are those of many of the other districts, since it is distinguished from the adjoining Mixed-grass Plains principally by having floral and faunal peculiarities which gradually diminish toward the northern and eastern limits of the district. The contact of this district with the Short-grass Plains district occurs outside of Oklahoma.

Physiography and geology: The Oklahoma section of this district is a part

of the Gypsum Hills physiographic region. The surface is level or rolling and slopes gently toward the Red River on the south. The average elevation above sea-level is about 1,500 feet. The soil is deep and fertile, and mostly under cultivation; but extensive areas on the uplands, especially near the Texas line in western Harmon County, are unusued except for grazing, and are apparently in almost original condition. The underlying rocks are horizontal beds of red shale, with some sandstone and gypsum strata which outcrop on the sides of the stream valleys, and in places form low bluffs facing the Red River valley. The gypsum strata contain a few caves. Near the streams the uplands are gullied in places, with steep clay slopes. The broad flood-plain of the Red River is in many places bordered by sand dunes, some of which are active. Extensive sand areas north of the river apparently represent older deposits of wind-blown sand from the flood-plain.

Climate: There are no weather stations in this district in Oklahoma; but Altus, a short distance northeast of the limits of the district, is probably representative (see p. 437).

Principal plant associations: This district is characterized by the abundance of thorny shrubs, including mesquite *(Prosopis glandulosa)* and such others as *Condalia obtusifolia* (Bruner, 1931, 181) and *Ephedra antisiphilitica* (Barkley and Barkley, 1933, 11), in an area of short grasses. The thorny shrubs sometimes form thickets, especially in the gullies, but are more often widely scattered on the uplands, with buffalo-grass *(Buchloë dactyloides)*, species of *Aristida*, and grama grasses forming the low ground cover. Clark (1934, 35) observed that a prickly pear *(Opuntia lepticaulis)* forms small, impenetrable thickets in this district, and listed other cacti, including *Echinocactus perbellus, E. texensis*, and *Opuntia davisii*.

Sand areas in this district have the types of plant associations that are developed in the Mixed-grass Plains district, including the cottonwood and willow zones along the streams, and the dune associations. *Scirpus* marshes occur about the sand-choked mouths of some of the creeks which enter the Red River.

Many of the characteristic animals of the Mesquite Plains district are evidently brought in through their direct association with the thorny shrubs which characterize the district. The most important of the shrubs in this respect is the mesquite, of which the foliage and particularly the seed-pods are fed upon by many animals. This plant transcends the limits of the Mesquite Plains district in Oklahoma (extending east at least to the Wichita Mountains and northwest to Tesesquite Creek in Cimarron County), but it is relatively scarce outside of the Mesquite Plains district.

Short-grass Plains Biotic District

Location: This district includes the Panhandle except the Mesa de Maya, and the northwestern corner of the main part of the state. It extends northward in Kansas and eastern Colorado, and southward in the Texas Panhandle. The eastern boundary is generally formed by a distinct scarp, rising rather abruptly from the level of the Mixed-grass Plains. The scarp shows many

re-entrants and projecting interstream prominences and outliers, but in most places constitutes a sharp and easily distinguishable boundary between the two districts.

Physiography and geology: This district lies in the High Plains physiographic region, and is a relatively level plain that slopes toward the southeast. The elevation varies from about 4,000 feet in the west to about 1,500 feet in the east. It is drained by tributaries of the Cimarron and Canadian Rivers, which have cut narrow, V-shaped valleys in the plain. The rocks are mostly Permian formations overlain by Tertiary sands, gravels, and clays.

Climate: The average annual temperature varies from 58.7° F. (33 year record) at Woodward, near the eastern limit of the region, to 53.9° F. (23 year record) at Boise City, near the western end of the Panhandle. The average annual rainfall drops from 25.10 inches (37 year record) at Woodward to 22.39 inches (21 year record) at Boise City. The growing season is longer in the eastern part of the district, being 206 days (30 year record) at Woodward compared to 180 days (23 year record) at Boise City.

Principal plant associations: The level plains are covered by short grasses. Blue grama *(Bouteloua gracilis)* and buffalo-grass *(Buchloë dactyloides)* were listed by Shantz (1923, 93), and hairy grama *(Bouteloua hirsuta)* was added to these as an important dominant by Bruner (1931, 180). This association bears a superficial resemblance to a well-mowed lawn, because of the low stature of the grasses. In many places these grasses form a continuous sod, while in others they are scattered with intervening areas of bare soil. Shantz *(loc. cit.)* mentioned a plaintain *(Plantago purshii)*, fescue *(Festuca octoflora)*, and stick-tight *(Lappula occidentale)* as small annuals that occur in this association.

Sandy areas along the streams have plant communities similar to those on sandy soil in the northern part of the Mixed-grass Plains district. There are scattered cottonwoods *(Populus deltoides)* along the margins of the streams. On the slopes of some of the creek valleys *Artemisia* and *Yucca* are the most conspicuous plants, with thickets of wild plums on the bottom lands, and willows and sedges along the creek banks. Steep ravine slopes, on which there are often outcrops of gypsum or sandstone, have scattered junipers and yuccas. The herbs and grasses in the valleys are taller than those of the level plains. Shallow ravines often have a conspicuous cover of kindling weed *(Amphiachyris dracunculoides)*.

The widespread movements of wind-blown soil in reecnt years have resulted in extensive areas on the uplands that bear no sign of plant or animal life. The most extensive of these areas lie in the central part of the Panhandle.

Mesa de Maya Biotic District

Location: The Mesa de Maya of New Mexico and Colorado extends into Oklahoma only in the northwestern corner of the Panhandle, where it is locally known as Black Mesa.

Physiography and geology: A system of deep canyons has been cut into the

Dakota sandstone in northwestern Cimarron County by the Cimarron River and its tributaries. In an area of six square miles the sandstones are covered with 100 feet or more of basaltic lava. The lava flow extends into Oklahoma from northeastern New Mexico and southern Colorado. The height of the lava-capped table-land and of some of the sandstone-capped erosional remnants is about 500 feet above the valley of the Cimarron River. The highest point on the Mesa de Maya in Oklahoma is almost 5,000 feet above sea level. The steep slopes below the lava cap are littered with angular talus fragments, and the sandstone slopes have large sandstone blocks. There is a permanent spring in a shallow canyon on one of the slopes.

Climate: The average annual temperature at Kenton is 54.8° F. (31 year record), and the average annual rainfall is 17.94 inches. The average length of the growing season is 179 days. The temperature rarely goes above 100° F. in summer, and in winter it may go to 18° below zero during blizzards.

Principal plant associations: The level plain on top of the Mesa de Maya does not differ from the other areas of short-grass plain already described, except for the presence of abundant lava fragments scattered over its surface toward the rim of the mesa. However, the ravine systems and the slopes of the Mesa de Maya escarpment and those formed by the erosion of the Dakota sandstone have a biota that is closely related to that of the foothills of the southern Rocky Mountains. The rock-littered slopes are covered in many places with a low scrub that seldom exceeds 4 or 5 feet in height. This scrub is formed chiefly by thick-leaved hackberry *(Celtis reticulata),* with which juniper *(Juniperus monosperma)* is sparsely intermixed. On north-facing slopes of the sandstone outcrops the junipers grow with pinyon pine *(Pinus edulis)* in stands that are occasionally quite thick, but which generally are sparse and frequently interrupted by large sandstone blocks. Live oaks also occur on the slopes with the evergreens. These oaks were identified by Paul C. Standley and recorded by Ortenburger (1928a, 51) as *Quercus undulata.*

The bed of the permanent trickle of water on the slope of the mesa has a few moist spots of soil on which thick mats of grass and herbs are found. The trees are those of the dry slopes, but they are more numerous along the stream.

Paul C. Standley identified and Ortenburger *(op. cit.,* 52) listed a variety of the silver beardgrass *(Andropogon saccharoides* var. *laguroides),* blue grama *(Bouteloua gracilis),* hairy triodia *(Triodia pilosa),* common bulrush *(Scirpus validus)* from the Mesa de Maya district. The mesa slopes are extremely barren of ground cover because of their rocky nature. There are extensive clumps of prickly pear *(Opuntia* sp.) and occasional plants of an arborescent species of cactus. The talus slopes below the lava cap are relatively barren of vegetation.

Discussion

From the foregoing description of the biotic districts in Oklahoma, it is evident that many of the plant associations and physiographic features are

present in several of the districts. Furthermore, an association or physiographic form may be the most characteristic feature of one district, and it may occur also as a minor feature in several other districts. The extension of suitable habitat types beyond the district in which they are dominant permits the extension of various animals into several districts. The fox squirrel, for instance, is widely distributed in the forest districts of eastern Oklahoma, but it extends westward across the Mixed-grass Plains district, which is dominated by grassland associations, by way of the narrow strip of flood-plain forest along some of the streams.

Since the distribution of the various habitat types in the biotic districts is of major importance in controlling the distribution of the animals, the distribution and relative importance of the habitat types in the various districts is shown in Table 1. Since no quantitative measure of the extent of the various habitat types has been made, this diagram undoubtedly contains a considerable subjective element. However, it does aid in clarifying the problem of animal distribution in Oklahoma.

The distribution of the mammals of Oklahoma has been treated in detail by Blair in a paper soon to be published. A study of the Orthoptera of the state in which the distribution of these insects in relation to the biotic districts will be discussed is in preparation by Hubbell. The following summaries will suffice to show how the distribution of these two groups of animals reflects the ecological pattern of the state which has been described above.

The Orthoptera

The Orthopteran fauna of Oklahoma comprises approximately 254 species and races, counting a number that certainly occur in the state, having been taken just beyond its boundaries. The species range in habits from burrowing to arboreal, and their distribution is consequently subject to a wide variety of controlling factors. Some of the species occupy micro-habitats that occur throughout the region, and others are so adaptable that they occur in a variety of habitat types and have very wide ranges. For the purpose of this discussion no consideration need be given to 20 forms with ranges that extend beyond the state in all directions, to 8 introduced species, nor to 11 others of sporadic occurrence that are too little known to permit analysis of their distribution.

The remaining 215 species and races (approximately 85% of the total fauna, or 91% of the fauna exclusive of adventives and sporadics) find eastern or western limits of distribution within the state. They may be classed with respect to their ranges as follows: *Eastern* — 90 species and races (35.4%) the ranges of which enter Oklahoma from the northeast, east, or southeast and reach western limits in the state; *Western* — 89 species and races (35%) the ranges of which enter from the northwest, west, or southwest and reach eastern limits in the state; *Plains*—32 species and races (12.6%) the ranges of which extend into or across the state from north or south, and have

both eastern and western limits in Oklahoma; and *Endemic* — 4 species or races (1.6%) the known ranges of which lie entirely within the state.

In contrast to the pronounced east-west zonation of the Orthopteran fauna, its changes from north to south are gradual and relatively slight. Disregarding the endemics, only 62 species and races (24.4% of the total fauna, or 26.4% of the fauna exclusive of adventives and sporadics) reach northern or southern limits within the state. Of the 90 eastern forms, 14 reach northern, 13 southern limits in Oklahoma, while 63 (70%) extend through the state. Of the 89 western species and races, 6 reach northern, 13 southern limits, while 67 (75%) extend beyond in both directions. Of the 32 plains species and races, 11 reach northern limits and only 1 a southern limit in Oklahoma, the remaining 20 (63%) ranging into Kansas and Texas. These figures make it evident that the marked east-west precipitation gradient is the predominant factor indirectly controlling the distribution of the Orthoptera of this area, with temperature playing a very subordinate role.

By plotting the generalized limits of distribution in Oklahoma, all of the eastern limits on one map and all of the western limits on another, the major limiting zones are prominently displayed. For the most part they correspond closely with the boundaries of the districts described above. However, the districts are of unequal importance in limiting distribution, and the same district boundary affects western and eastern species in different degrees. Thus the boundary between the Osage Savanna and the relatively treeless Mixed-grass Plains district determines the western limit of nearly one-third of the eastern species, whereas only about 15% of the western species terminate at this zone.

Considering the eastern species, the most important limiting zones are those of the western edges of the Ozark, Ouachita, Mississippi, and Osage Savanna districts. Along the northern border of the state the proportions of the eastern fauna terminating in the vicinity of the different boundaries are approximately as follows: Ozark-Cherokee, 15%; Cherokee-Osage, 8%; Osage-Mixed-grass, 28%. The 51% of the eastern fauna which does not extend much beyond the last-named boundary includes practically all of the forest-inhabitants, as well as some others. The eastern species which range farther west are inhabitants of thickets, herbage, grassland, bare ground, and various special situations, such as the edges of ponds and streams, and the soil. They are not so sharply zonal in distribution, and drop off one by one, though a considerable number of ranges stop at or near the margin of the Short-grass Plains. In the south the forest-loving species characteristic of the Osage Savanna are carried far westward by the Wichita Mountains.

The map of the eastern limits of western species shows a similar distribution of limiting zones, but a smaller proportion of the fauna terminates at any given zone. About 15% of the western species belong to the fauna of the southern Rocky Mountains, and enter the state only in the pinyon-juniper belt on the slopes of the Mesa de Maya. Many of the species abundant in the Short-grass Plains have ranges which are bounded at or west of the east-

ern margin of this district (17%). Many others enter the Mixed-grass Plains district; 25% of the western group find their eastern limits somewhere within this district, while 15% reach the edge of the Osage Savanna. The species which extend farther east are mostly limited by the edge of the Ozark district. In both eastern and western groups a few species, that have ranges lying to the north or south of Oklahoma, in this area have oblique limits which suggest the combined effects of humidity and temperature.

The Mixed-grass Plains district is essentially a transition zone between the xerophile biota of the Short-grass Plains and the mesophile biota of the tall-grass prairies and eastern forests. Its Orthopteran fauna is made up chiefly of Short-grass Plains species occupying the more xeric habitat types, and of eastern species in the moister situations. The Mesquite Plains district Orthopteran fauna is likewise transitional, though its closest affinities are with that of the Short-grass Plains; in addition it possesses a few species of southwestern affinities that do not occur elsewhere in the state. The remaining districts are comparatively distinct, and each possesses a characteristic assemblage of Orthopteran species.

Species limited to single districts are found only in the Ozark, Mississippi, Wichita Mountain, Mesquite Plains, and Mesa de Maya districts. The distinctions between the Orthopteran faunas of the various districts lie chiefly in the presence or absence of particular species, and in the preponderance of those characteristic of the dominant habitat types in each district. Without extended treatment it is impossible adequately to characterize the different faunas. Instead of attempting to do so, species considered characteristic of each district are listed below. Those common to most or all of the districts are omitted, even though they may be abundant and form an important element in the fauna of certain districts. Species of sporadic occurrence are generally not included. Species which in Oklahoma are limited to a single district are indicated by capitals, and are also starred when endemic. Square brackets indicate species almost certain to occur in but not yet recorded from a district.

Ozark district: The cockroaches *Ischnoptera deropeltiformis, Parcoblatta zebra, P. uhleriana, P. virginica,* [*P. lata*]; the walking-sticks DIAPHEROMERA BLATCHLEYI, [*D. femorata, Megaphasma denticrus*]; the cricket-locusts *Ceuthophilus seclusus, C. divergens,* [C. G. GRACILIPES, C. *ozarkensis*]; the crickets *Miogryllus verticalis, Nemobius bruneri, N. c. carolinus,* [*Oecanthus angustipennis, O. niveus, O. latipennis, Neoxabea bipunctata, Hapithus a. agitator, Orocharis saltator*]; the katydids *Amblycorypha uhleri, Pterophylla camellifolia;* the short-horned grasshoppers *Dichromorpha viridis,* [CHLOEALTIS CONSPERSA], *Arphia sulphurea, Spharagemon bolli, Trachyrhachis kiowa fuscifrons, Schistocerca d. damnifica,* [MELANOPLUS GRACILIS], *M. ponderosus viola,* [*M. impudicus, M. fasciatus,* possibly M. BOREALIS JUNIUS]; the grouse-locust *Tettigidea lateralis parvipennis.*

Ouachita district: The cockroaches *Ischnoptera deropeltiformis, Parcoblatta virginica, P. caudelli, P. lata;* the mantid *Oligonicella scudderi;* the walking-sticks [*Diapheromera femorata*], *Megaphasma denticrus;* the cricket-locusts *Ceuthophilus seclusus,* [*C. ozarkensis*], *C. divergens;* the crickets *Miogryllus verticalis,* [*Nemobius c. carolinus*], *Oecanthus angustipennis,* [*O. latipennis, Orocharis saltator*]; the katydids *Amblycorypha uhleri, Pterophylla furcata, Neoconocephalus triops;* the short-horned grasshoppers *Mermiria picta, Amblytropidia occidentalis, Dichromorpha viridis, Arphia*

sulphurea, Spharagemon bolli, Trachyrhachis kiowa fuscifrons, Trimerotropis saxatilis, [*Schistocerca d. damnifica*], *Paratylotropidia brunneri, Melanoplus r. rusticus, M. plebejus, M. inconspicuus, M. ponderosus viola, M. impudicus;* the grouse-locusts *Neotettix femoratus, Tettigidea l. lateralis, T. armata.*

Mississippi district: The cockroaches *Ischnoptera deropeltiformis, Parcoblatta zebra, P. virginica, P. lata,* P. DIVISA; the mantid [*Oligonicella scudderi*]; the walking-stick ANISOMORPHA FERRUGINEA; the cricket-locust *Ceuthophilus divergens;* the crickets *Miogryllus verticalis,* [*Anurogryllus muticus*], *Nemobius c. carolinus, Oecanthus angustipennis, O. latipennis,* [*Orocharis saltator*], *Hapithus agitator quadratus,* [possibly CYCLOPTILUM TRIGONIPALPUM and C. BIDENS]; the katydids *Amblycorypha p. parvipennis, Pterophylla furcata, Neoconocephalus triops,* ATLANTICUS AMERICANUS HESPERUS;[1] the short-horned grasshoppers [*Mermiria picta*], *Dichromorpha viridis, Arphia sulphurea, Spharagemon bolli,* [*Schistocerca d. damnifica*], *Melanoplus r. rusticus, M. plebejus,* M. OKLAHOMAE;* the grouse-locusts [*Neotettix femoratus*], *Tettigidea l. lateralis, T. armata.*

Cherokee Prairie district: The walking-stick *Diapheromera v. velii;* the cricket-locusts *Ceuthophilus seclusus, C. pallidus,* C. *nodulosus;* the mole-cricket *Gryllotalpa major;* the katydids *Amblycorypha huasteca, A. uhleri, A. parvipennis brachyptera, Pediodectes haldemanii;* the short-horned grasshoppers *Mermiria bivittata, Dichromorpha viridis, Boöpedon auriventris, Arphia sulphurea, Trachyrhachis kiowa fuscifrons, Melanoplus inconspicuus, M. impudicus;* the grouse-locust *Tettigidea lateralis parvipennis.*

Osage Savanna district: The cockroaches *Ischnoptera deropeltiformis, Parcoblatta caudelli, P. lata,* and in the southern third *Pseudomops septentrionalis* and *Arenivaga tonkawa;* the mantid *Oligonicella scudderi;* the walking-sticks *Diapheromera persimilis, D. v. velii;* the cricket-locusts *Ceuthophilus nodulosus, C. seclusus* in the north, C. OSAGENSIS* in the south, C. *conicaudus* and C. UMBRATILIS; the crickets *Miogryllus verticalis, Anurogryllus muticus,* [*Nemobius bruneri*], *Trigonidomimus belfragei, Oecanthus angustipennis, O. latipennis, Gryllotalpa major;* the katydids ARETHAEA GRALLATOR, *Amblycorypha huasteca, A. uhleri, A. parvipennis* (probably race *brachyptera* in the north, race *parvipennis* in the south), *Neoconocephalus triops;* the short-horned grasshoppers *Boöpedon auriventris, Arphia sulphurea, Leprus wheeleri, Spharagemon bolli, Trachyrhachis kiowa fuscifrons, Trimerotropis saxatilis, Schistocerca d. damnifica, Paratylotropidia brunneri,* MELANOPLUS BEAMERI in the north (Bragg MS), *M. plebejus* in the south, *M. texanus, M. inconspicuus, M. ponderosus viola* atypical, *M. impudicus, M. fasciatus* in the north (Bragg MS), *M. foedus iselyi, Dendrotettix quercus;* the grouse-locust *Tettigidea lateralis* (atypical race *parvipennis* in the north, grading toward *lateralis* southward.)

Wichita Mountain district: The cockroaches *Ischnoptera deropeltiformis, Parcoblatta desertae, Pseudomops septentrionalis, Arenivaga tonkawa;* the cricket-locusts *Ceuthophilus conicaudus, C. pallidus,* C. WICHITAENSIS;* the crickets *Nemobius carolinus brevicaudus, Hapithus agitator quadratus;* the katydids *Arethaea ambulator, Amblycorypha huasteca, Rhenia victoriae, Pediodectes haldemanii, P. nigromarginata; the short-horned grasshoppers Pseudopomala brachyptera, Phlibostroma quadrimaculatum, Psoloessa t. texana, Boöpedon auriventris, Arphia sulphurea, Leprus wheeleri, Spharagemon bolli, Trimerotropis saxatilis,*[2] T. PALLIDIPENNIS endemic race,* *Melanoplus texanus, M. p. ponderosus, M. arizonae, M. regalis, M. foedus iselyi.*

---

1 This species may also be present in the Ozark and Ouachita districts.

2 Previous records of *T. saxatilis* from Oklahoma are in part correct, in part based on material of the endemic race of *T. pallidipennis* next mentioned, which superficially resembles *saxatalis.* Although local, being confined to rock ledge habitats in forested areas, *T. saxatilis* has a wider geographic range in the state than does the endemic race of *T. pallidipennis.* The latter is as yet known only from the Wichita Mountain district, though it may also occur in southern part of the Osage Savanna district.

Mixed-grass Plains district: The mantid *Litaneutria minor;* the walking-sticks *Diapheromera persimilis, D. v. velii;* the cricket-locusts *Ceuthophilus conicaudus, C. pallidus, C. nodulosus, Daihinia brevipes, Ammobaenetes* sp. (in sand areas); the crickets *Gryllus assimilis* ecological phase *personatus* (in sand areas), *Gryllotalpa major;* the katydids *Amblycorypha huasteca, Orchelimum concinnum delicatum, Rehnia victoriae, Pediodectes haldemanii, P. nigromarginata;* the short-horned grasshoppers *Pseudopomala brachyptera, Mermiria neo-mexicana, M. maculipennis* approaching race *mcclungi, Acrolophitus hirtipes, Syrbula fuscovittata, Phlibostroma quadrimaculatum, Psoloessa t. texana, Aulocara elliotti, Boöpedon nubilum, Arphia c. conspersa, Encoptolophus pallidus subgracilis, E. sordidus costalis, Mestobregma p. plattei, Trimerotropis pallidipennis salina, T. agrestis* (in sand areas in north), *T. laticincta, Circotettix rabula nigrafasciatus* in the north, *Hypochlora alba, Melanoplus glaucipes, M. arizonae, M. regalis, M. foedus iselyi, Dactylotum pictum.*

Mesquite Plains district: The cockroach *Parcoblatta desertae;* the mantids *Yersiniops solitarium, Litaneutria minor;* the walking-sticks *Pseudosermyle straminea, Diapheromera v. velii;* the cricket-locusts *Ceuthophilus conicaudus, C. pallidus, Daihinia brevipes;* the katydids DICHOPETALA EMARGINATA,* ARETHAEA GRACILIPES atypical; *Rehnia victoriae;* the short-horned grasshoppers *Pseudopomala brachyptera, Mermiria neo-mexicana, M. maculipennis* atypical, *Acrolophitus hirtipes, Opeia obscura, Phlibostroma quadrimaculatum, Cordillacris o. occipitalis, Drepanoptera femoratum, Aulocara elliotti, Boöpedon nubilum, Arphia c. conspersa, A. pseudonietana, Trimerotropis p. pallidipennis, T. p. salina, T. pistrinaria, T. laticincta, Hypochlora alba, Aeoloplus turnbulli bruneri, Melanoplus glaucipes, M. p. ponderosus, M. arizonae, M. regalis, M. lakinus, M. b. bowditchi, Dactylotum pictum.*

Short-grass Plains district: The cockroach Parcoblatta desertae; the mantid *Litaneutria minor;* the walking-sticks *Parabacillus coloradus, Diapheromera v. velii;* the cricket-locusts *Ceuthophilus pallidus, Daihinia brevipes;* the crickets *Gryllus assimilis* ecological phase *personatus* (in sand areas), *Nemobius c. brevicaudus, Cycloptilum c. comprehendens;* the katydids *Orchelimum concinnum delicatum, Rehnia victoriae* in the eastern part, *Pediodectes haldemanii, P. stevensonii;* the short-horned grasshoppers *Mermiria neo-mexicana, M. maculipennis* near race *mcclungi, Acrolophitus hirtipes, Syrbula fuscovittata, Opeia obscura, Amphitornus c. coloradus,* ERITETTIX SIMPLEX TRICARINATUS,[3] *Phlibostroma quadrimaculatum, Cordillacris o. occipitalis,* C. CRENULATA,[3] *Psoloessa t. texana,* P. D. DELICATULA,[3] *Drepanoptera femoratum, Aulocara elliotti, Boöpedon nubilum, Arphia c. conspersa, A. pseudonietana, Encoptolophus pallidus subgracilis, E. sordidus costalis,* XANTHIPPUS CORALLIPES LATEFASCIATUS[3] (in the west), X. MONTANUS[3] (in sand areas), TROPIDOLOPHUS FORMOSUS,[3] DEROTMEMA H. HAYDENII,[3] REHNITA CAPITO,[3] *Trachyrhachis k. kiowa, Mestobregma p. plattei, Trimerotropis p. pallidipennis, T. p. salina, T. agrestis* (in sand areas), *T. pistrinaria, T. laticincta,* [T. MAGNIFICA, *Circotettix rabula nigrafasciatus*], *Parapomala wyomingensis, Hypochlora alba,* CAMPYLACANTHA OLIVACEA VIVAX,[3] *Aeoloplus turnbulli bruneri, Melanoplus discolor, M. glaucipes, M. regalis, M. lakinus,* M. O. OCCIDENTALIS,[3] M. F. FOEDUS,[3] *M. b. bowditchi, Dactylotum pictum.*

Mesa de Maya district: In addition to the Short-grass Plains species, most of which occur in this district, the pinyon-juniper zone on the rocky slopes of the Mesa de Maya is inhabited by a number of species characteristic of the southern Rocky Mountains and the arid southwest, that occur nowhere else in Oklahoma. These are: the mantid STAGMOMANTIS LIMBATA; the cricket-locust CEUTHOPHILUS UTAHENSIS; the cricket OECANTHUS C. CALIFORNICUS; the katydids ARETHAEA G. GRACILIPES and CAPNOBOTES FULIGINOSUS; the short-horned grasshoppers MERMIRIA TEXANA, HELIAULA RUFA, LEPRUS CYANEUS, and MELANOPLUS SPLENDIDUS. The mantid *Yersiniops solitarium* and the walking-stick *Pseudosermyle straminea,* also characteristic of the district, are known elsewhere in the state only from the Mesquite Plains district.

---

3 Though indicated as confined to the Short-grass Plains district, these species occur also in identical habitats in the Mesa de Maya district.

The Mammals

Seventy-three species of mammals have been recorded from Oklahoma. Some of the species are represented by more than one race, so that there are 91 species and races of mammals known from the state. Twenty-four (33%) of the 73 are wide-ranging species, of which the ranges extend beyond the state in all directions. The ranges of 3 species (4%) are unknown. Twenty-two (30%) of the species are eastern forms that reach the western limits of their ranges in Oklahoma. An exactly equal number are species of western distribution that reach their eastern limits in the state. There is, then, a great change in the mammalian fauna as one passes from east to west in the state, with 60% of the species reaching either eastern or western limits.

Northern limits of distribution are reached in Oklahoma (or in extreme southern Kansas) by only 6 (8%) of the 73 species in the state, and southern limits are reached by only two (3%) of the species. It is evident, then, that there is a much greater change in the mammalian fauna in an east-west direction across the state than in a north-south direction. This in turn makes it apparent that the principal factor influencing mammalian distribution in Oklahoma is the amount of precipitation, acting indirectly through its control of plant associations. Temperature, on the other hand, is of little importance as a limiting factor, since only 11% of the species of mammals reach northern or southern limits within the state.

The limits of the various species in many cases approximate the limits of the various biotic districts in the state, although numerous species transcend the district boundaries. Of the 22 species of eastern distribution that reach wesern limits in the state, 7 (32%, or 10% of the species in the state) reach their western limits at the approximate western limits of the Ozark, Ouachita, and Mississippi districts. The 15 remaining species reach their western limits at various places in the Osage Savanna, Wichita Mountain, and Mixed-grass Plains districts. So far as known these species do not extend westward beyond the approximate western border of the Mixed-grass Plains district.

Of the 22 western species that reach eastern limits in the state, 5 (23%, or 7% of the species in the state) belong to the fauna of the southern Rocky Mountains, and extend into the state only in the Mesa de Maya district. The other western species are, for the most part, grassland species that range over both the Short-grass Plains and Mixed-grass Plains districts. These species reach their approximate eastern limits at the eastern boundary of the Osage Savanna district.

Of the 6 species that approach northern limits in the state, 5 are eastern forest species that reach western limits in Oklahoma, and the other is transcontinental in distribution. One of the 6 is limited by the northern boundary of the Mississippi district; two by the northern boundary of the Ouachita district, and two by the northern boundary of the Ozark district. The other species reaches its northern limit somewhere in southern Kansas. The two

northern species that reach southern limits do not extend south of the Cherokee Prairie district.

From the preceding discussion, it is evident that there are 3 principal mammalian faunas represented in Oklahoma. One of these is the fauna of the eastern deciduous forest which is represented in the Ozark, Ouachita, and Mississippi biotic districts, and which is seriously limited westward by the boundaries of those districts. This fauna is found in an attenuated form in the Osage Savanna, Wichita Mountain, and Mixed-grass Plains districts. Another mammalian fauna is that of the southern Rocky Mountains, which just enters the northwestern corner of the Panhandle and is limited by the eastern boundary of the Mesa de Maya district. The other fauna is that of the grasslands of the Great Plains, and ranges over the Mixed-grass Plains, Short-grass Plains, and Mesquite Plains districts. An attenuation of this fauna occurs in the Osage Savanna district.

The principal faunal differences between the Mixed-grass Plains and Short-grass Plains districts are the result of raciation in species that range over both districts. Four species are represented by dark-colored races on the dark, reddish soils of the Mixed-grass Plains, and by pale-colored races on the pale soils of the Short-grass Plains. The presence of its attenuated eastern forest fauna also serves to distinguish the Mixed-grass Plains from the Short-grass Plains district.

Since the distribution of the mammals in Oklahoma will be treated in a forthcoming paper, only a brief statement about a few of the most characteristic species of each district will be made here.

Ozark district: Most of the mammals of the Ozark district have their affinities with the mammalian fauna of the eastern deciduous forest. The chipmunk *(Tamias striatus venustus)* and woodchuck *(Marmota monax monax)* are the most characteristic mammals of this district. The western limits of these forms closely approximate the western boundary of the district, but southward they probably extend for some distance into the Ouachita district. The deermouse *(Peromyscus maniculatus ozarkiarum)* which occupies grassland habitats in the Ozark district, is not known to occur in the Ouachita district. A brown cave bat *(Myotis grisescens)* in Oklahoma is known only to occur in the Ozark district.

Ouachita district: The mammals of the Ouachita district, like those of the Ozark district, are eastern in their affinities, and the fauna differs from that of the Ozark district chiefly in the presence of southeastern species that do not extend northward into the Ozark district. The cotton-mouse *(Peromyscus gossypinus megacephalus)*, golden mouse *(Peromyscus nuttallii aureolus)*, and evening bat *(Nycticeius humeralis)* are characteristic of the Ouachita district.

Mississippi district: The mammals of this district are those of the humid Gulf coastal plain and lower Mississippi valley, and many of the species that occur in this district extend northward into the Ouachita district. The swamp

rabbit *(Sylvilagus aquaticus aquaticus)* is one of the most abundant and widely distributed mammals of the Mississippi district. It extends northward and westward of the district, but in so doing it becomes restricted to the floodplains of the streams, so that it is a minor constituent of the fauna. The rice rat *(Oryzomys palustris texensis)* is the only species of mammal that has been recorded in Oklahoma only from the Mississippi district.

Cherokee Prairie district: The Cherokee Prairie biotic district is characterized by the occurrence on the grassy uplands of the deermouse *(Peromyscus maniculatus ozarkiarum)*, prairie vole *(Microtus ochrogaster)*, and cotton-rat *(Sigmodon hispidus texianus)*. The stream valleys are occupied by eastern forest species, of which the gray squirrel *(Sciurus carolinensis carolinensis)*, fox squirrel *(Sciurus niger rufiventer)*, pine vole *(Pitymys nemoralis)*, woodmouse *(Peromyscus leucopus noveboracensis)*, and Carolina shrew *(Blarina brevicauda carolinensis)* are representative.

Osage Savanna district: The Osage Savanna is characterized by the interdigitation of eastern deciduous forest species of mammals in the forest associations with species of western distribution in the grassland associations. Representative of the forest species are the Florida woodrat *(Neotoma floridana baileyi)*, wood-mouse *(Peromyscus leucopus noveboracensis)*, and swamp rabbit *(Sylvilagus aquaticus aquaticus)*. Representative of the western grassland species are the plains pocketmouse *(Perognathus hispidus spilotus)*, gray harvest-mouse *(Reithrodontomys montanus griseus)*, and black-tailed jackrabbit *(Lepus californicus melanotis)*.

Wichita Mountain district: The mammals of the forested parts of the Wichita Mountain district constitute a somewhat attenuated eastern deciduous forest fauna that does not differ greatly from the fauna of the forested parts of the Osage Savanna district. Species of mammals which occur in the Wichita Mountain district, but which are absent from the surrounding Mixed-grass Plains district, or are confined there to a narrow area along the streams, include the fox squirrel *(Sciurus niger rufiventer)*, pine vole *(Pitymys nemoralis)*, golden harvest-mouse *(Reithrodontomys fulvescens intermedius)*, and woodmouse *(Peromyscus leucopus texanus)*.

Mixed-grass Plains district: Most of the mammals of the Mixed-grass Plains district are grassland species that range widely on the Great Plains. The plains pocketmouse is represented in this district by a dark-colored race *(Perognathus hispidus spilotus)* and the thirteen-lined spermophile by a dark, reddish race *(Citellus tridecemlineatus texensis)*. The grasshopper mouse is represented by a dark-colored race *(Onychomys leucogaster breviauritus)* and the plains woodrat by a relatively dark race *(Neotoma micropus micropus)*. A kangaroo rat *(Dipodomys ordii richardsoni)* is a characteristic species on sandy soil.

Mesquite Plains district: Little is known about the mammalian fauna of the Mesquite Plains district, but it probably does not differ greatly from that of the Mixed-grass Plains district.

Short-grass Plains district: Most of the species of mammals of the Short-

grass Plains, like those of the Mixed-grass Plains district are widely distributed over the Great Plains. The plains pocketmouse is represented in the Short-grass Plains district by a pale-colored race *(Perognathus hispidus paradoxus)*, the thirteen-lined spermophile by a pale-colored race *(Citellus tridecemlineatus arenicola)*, the grasshopper mouse by a pale-colored race *(Onychomys leucogaster arcticeps)*, and the plains woodrat by a relatively pale race *(Neotoma micropus canescens)*. The swift *(Vulpes velox velox)* is a characteristic species of the Short-grass Plains district.

Mesa de Maya district: At the eastern border of the Mesa de Maya biotic district several southern Rocky Mountain species of mammals reach their eastern limits. Among these are the western chipmunk *(Eutamias quadrivittatus quadrivittatus)*, cliff mouse *(Peromyscus nasutus nasutus)*, white-throated woodrat *(Neotoma albigula warreni)*, mule-eared bat *(Antrozous pallidus)*, and a brown bat *(Myotis subulatus melanorhinus)*.

Summary

Ten biotic districts are distinguishable in Oklahoma. The Ozark, Ouachita, Mississippi, and Cherokee Prairie districts are a part of the eastern deciduous forest. The Osage Savanna district is an area of transition from the eastern deciduous forest to the grasslands of the Great Plains. The Wichita Mountain district is an outlier of the eastern deciduous forest in the Great Plains grasslands. The Mixed-grass Plains, Mesquite Plains, and Short-grass Plains are biotic districts of the Great Plains grasslands. The Mesa de Maya district belongs with the southern Rocky Mountains.

The Orthoptera and mammals of Oklahoma agree in showing little north-south zonation, but marked east-west zonation, indicating that precipitation and not temperature is the most important factor controlling (although indirectly) the distribution of these groups in Oklahoma. Edaphic factors largely control the distribution of habitat types in the various districts, and permit the westward extension of forest plant associations and animal species, and the eastward extension of grassland plant associations and animals.

The western limits of the eastern forest districts are of major importance in limiting the westward distribution of eastern species of Orthoptera and mammals. Likewise is the eastern limit of the Mesa de Maya district important in limiting the eastward distribution of southern Rocky Mountain species. The boundaries of the other districts are of somewhat less importance in limiting the distribution of species. From this it is evident that three major Orthopteran and mammalian faunas are represented in Oklahoma—an eastern fauna in the eastern deciduous forest districts, a southern Rocky Mountain fauna in the Mesa de Maya district, and a Great Plains grassland fauna in the intervening districts.

The various districts are distinguishable *inter se* by characteristic physiographic features and plant associations, by characteristic species of Orthoptera, by characteristic species and races of mammals, and by characteristic assemblages of species of Orthoptera and mammals.

TABLE 1

The distribution of habitat types in the biotic districts in Oklahoma. The estimated extent of each habitat type in each district in relation to the extent of the other habitat types in the district is indicated by the number of check marks. The maximum of 5 checks indicates that the habitat type is of major extent in the district, and the estimated extent of the habitat type decreases with the number of checks.

		HABITAT TYPES	BIOTIC DISTRICTS									
			Mesa de Maya	Short-grass Plains	Mesquite Plains	Mixed-grass Plains	Wichita Mountain	Osage Savanna	Cherokee Prairie	Ozark	Ouachita	Mississippi
FOREST ASSOCIATIONS	Closed Forest	Mesic Soils — Mississippi flood-plain forest										xxx
		Mesic Soils — Ouachita flood plain forest									xx	
		Heavy Soils — Oak—elm flood-plain forest						x	x	x		
		Heavy Soils — Mesic ravine forest					xxx	x	x	x	xx	
	Open Forest	Heavy Soils — Open flood-plain forest					x	x	x	x	x	x
		Heavy Soils — Pine—sweetgum alluvial forest									x	xxx
		Thin Soils — Oak—yellow pine forest								x	xxxxx	x
		Thin Soils — Oak—hickory forest				x	xxxxx		x	xxxxx	xx	
		Sandy Soils — Blackjack forest					x	xxxxx				
		Sandy Soils — Cottonwood—willow association	x	xx	xxx	xxx	x	x	x	x	x	x
		Xeric Rock — Oak—juniper saxophile forest		x		x				xx	x	
		Xeric Rock — Pinyon—juniper saxophile forest	xxx									
SCRUB AND THICKET ASSOCIATIONS	Mesic or Wet	Flood-plain thickets					x	x	xx	xx	xx	xx
		Forest margin thickets	x	x		x	xx	xx	xx	xx	xx	xx
	Xeric	Dry thickets on heavy soil			x	x	x	x	xx	x	x	
		Shin-oak thickets on sand		x		xxx						
		Dry thickets on sand	x	x	x	xx	x					
		Dry thickets on shallow soils	x	x	x	x	x	x	x	x	x	
		Thorn scrub	x		xxxx							
		Canyon and rock-slope thickets	xxx	x		x	x	x				

GRASSLAND AND HERBAGE ASSOCIATIONS	Wet	Emergent vegetation	x	x	x	x	x	x	x	x	x	x
		Sedge, bulrush, cat-tail marshes	x	x	x	x	x	xx	xx	x	x	xx
		Wet meadows and seepage slopes	x	x		x	x	xx	x	xx	xx	xx
	Heavy	Rank herbage and weed thickets	x	x	x	x	x	x	x	x	x	x
	Deep Soil	Tall-grass association		x		xx	x	xx	xxxxx	xx	x	
	Sand	Bunch-grass on sand	x	xx	xx	xxx	x				x	
	Shallow or immature Soils	Mixed-grass association				xxxxx	xxxxx	xxxx	x			
		Grass—mesquite association			xxx	x	x					
		Dry weed fields on thin soil	xx	xx	xx	xx	x	x	x	x	x	x
		Sagebrush flats	x	xx	xx	xx						
		Short-grass association	xxxxx	xxxxx	x	x	x	x	x			
BARE OR SPARSELY VEGETATED SOIL	Wet	Sand bars, muddy stream banks	x	x	x	x	x	x	x	x	x	x
		Pond margin mud flats	x	x	x	x	x	x	x	x	x	x
		Deep alluvial and mature residual soils			x		x	x	xx	x	x	xx
	Sand	Salt flats				xx						
		Dry sandy soil	xx	xx	x	xx	x	x	x	x	x	x
	Thin	Shallow, stony, immature or eroded soils	xxxx	xx	x	xx	xx	x	x	x	x	
		Rock ledges and cliffs	xxx	x	x	x	xx	x	x	xx	xx	
HYPOGEIC HABITATS		Deep alluvial and mature residual soils			x		x	x	xx	x	x	xx
		Sandy soils	xx	xx	xx	xxx	x	xx	x	x	x	x
		Shallow, stony, immature, or eroded soils	xxx	xx	xx	xxx	xx	xx	x	xx	xx	
		Caves in limestone, gypsum, lava	x	x	x	x	x	x	x	xx		
Climate		Rainfall (inches)	18	22-25	20	27-32	31.5	38	37-43	42.4	42.52	45.4
		Temperature	54.8°	54-58°	63°	58-63°	62°	59-64°	60°	60.1°	63°	61.6°
		Growing season (days)	179	180-206	224	203-224	219	200-235	200-218	209	216	240

REFERENCES

BARKLEY, F. A. AND E. A. BARKLEY. 1933—Ephedra antisiphilitica Meyer, establishing another order of plants for Oklahoma. Proc. Okla. Acad. Sci. **13**:11-12.

BLAIR, W. F. 1938—The ecological relationships of the mammals of the Bird Creek region, northeastern Oklahoma. Amer. Midl. Nat. **20**(3).

BRAGG, J. H.—The Geographical Distribution of Acrididae in northern Oklahoma (unpublished thesis, University of Oklahoma, 1936).

BRUNER, W. E. 1931—The vegetation of Oklahoma. Ecol. Monogr. **1**:99-188.

CLARK, O. M. 1934—The cacti of Oklahoma. Proc. Okla. Acad. Sci. **14**:34-36.

———1935—Rare and unusual plants in Oklahoma. Proc. Okla. Acad. Sci. **15**:38.

GOULD, C. N. 1905—Geology and water resources in Oklahoma. U. S. Geol. Survey, Water-supply and Irrigation Paper **148**:1-178.

HEFLEY, H. M. 1937—Ecological studies on the Canadian River flood-plain in Cleveland County, Oklahoma. Ecol. Monogr. **7**:345-402.

LITTLE, E. A. 1936—Bryophytes and Pteridophytes of some west central Oklahoma canyons. Proc. Okla. Acad. Sci. **16**:47-52.

———AND C. E. OLMSTEAD. 1936—Trees and shrubs of the southeastern Oklahoma protective unit. Proc. Okla. Acad. Sci. **16**:52-61.

OKLAHOMA GEOLOGICAL SURVEY.—Bull. 40, **2**:1-501, **3**:1-663.

ORTENBURGER, A. I. 1928a—Plant collections representative of some typical communities of western Oklahoma. Proc. Okla. Acad. Sci. (Univ. Okla. bull., n.s., **410**:49-52).

———1928b—Plant collections representative of some typical communities of eastern Oklahoma. Proc. Okla. Acad. Sci. (Univ. Okla. bull., n. s. **410**:53-57).

PALMER, E. J. 1924—The ligneous flora of Rich Mountain, Arkansas and Oklahoma. Journ. Arnold Arboretum **5**:108-134.

SHANTZ, H. L. 1923—The natural vegetation of the Great Plains region. Annals Assoc. Amer. Geographers **13**:81-107.

SNIDER, L. C. 1917—Geography of Oklahoma. Okla. Geol. Survey **27**:1-325.

STEYERMARK, J. A. 1934—Some features of the flora of the Ozark region in Missouri. Rhodora **36**:214-233.

TURNER, L. M. 1935—Notes on forest types of northwestern Arkansas. Amer. Midl. Natur. **16**:417-421.

UNITED STATES WEATHER BUREAU. 1934—Climatic Summary of the United States. Sec. 42, 43.

Notes on the Den Ecology of the Striped Skunk in Iowa[1]

Lyle F. Selko

Den ecology studies of the striped skunk, *Mephitis mesomelas avia* (Bangs), in Iowa were begun in the fall of 1936. The results of the investigation as presented here span the period of time from the above mentioned season throughout the summer of 1937. The environment of 30 dens are included from the region of study which was located within a radius of twenty miles of Ames, and particularly on farms along Squaw Creek and Skunk River north of the city.

The research was under the supervision of Dr. Logan J. Bennett, Associate Biologist, U. S. Bureau of Biological Survey and Dr. George O. Hendrickson, Assistant Professor in Wildlife Management, Iowa State College.[2]

The data of the investigation as recorded herein are grouped in the following classification: (1) the pre-hibernation den environment of striped skunks in the fall of 1936; (2) the den environment of individual striped skunks in the spring and summer of 1937; and, (3) the den environment of striped skunk families in the spring and summer of 1937. Dens included in the first division of the classification are those which were selected by skunks for hibernation and were being prepared for the winter period. Den environment of individual striped skunks as recorded in the second division includes those dens which were occupied continuously by individuals for a period of at least two weeks. This latter category is for the purpose of doing away as much as possible with the factor of wandering skunks.

Pre-hibernation Den Environment of Striped Skunks in the Autumn of 1936

The twelve dens observed which are listed in Table 1 had nine, or 75 per cent, of their number on rolling or hilly land along creeks, and three, or 25 per cent, on comparatively level land quite close to rolling land. Nine of these dens had only one entrance with a quota of three openings to the northwest, four to the southeast, and one each to the west and southwest. The remaining three dens with several entrances had two openings facing the west and one facing the southwest, south, northeast, and north.

Woodchucks dug seven, or 58.33 per cent, of these dens; badgers and

---

1 Jour. Paper No. J-541 of the Iowa Agricultural Experiment Station. Project No. 549.

2 Iowa State College, in cooperation with the U. S. Biological Survey, the American Wildlife Institute, and the Iowa Conservation Commission.

TABLE 1

Pre-Hibernation Den Environment of Skunks in the Autumn of 1936* **

Den No.	Date First Observed	Land Site	No. of Entrances	Entrance Direction	Type of Den	Distance from water	Type of Water	Predominant Species Vegetation	Average Height	Amount of Grazing
1	Oct. 2	Hilly Creek	1	Southwest	Woodchuck *Marmota monax monax*	200(yds)	River	Hemp (*Cannabis sativa*) Bluegrass (*Poa pratensis*)	6 ft. 3 in.	Fairly Heavy
2	Nov. 6	Rolling	2	Southwest Northeast	Woodchuck	440	Creek	Greater ragweed (*Ambrosia trifida*) Sweetclover (*Melilotus* sp.)	5 ft.	None
3	Nov. 12	Rolling	1	Southeast	Woodchuck	440	River	Dropseed (*Sporobolus* sp.) Bluegrass	4 ft.	None
4	Nov. 12	Rolling	1	Southeast	Woodchuck	880	River	Dropseed Bluegrass	3 ft.	None
5	Nov. 12	Rolling	1	Southeast	Woodchuck	640	River	Dropseed Bluegrass	3 ft.	None
6	Nov. 13	Ridge of Lake	1	Northwest	Fox *Vulpes regalis*	50	Marsh	Bluegrass	1 ft.	None
7	Nov. 13	Ridge of Lake	1	West	Fox	50	Marsh	Bluegrass	4 in.	None
8	Nov. 13	Ridge of Lake	1	Southeast	Woodchuck	100	Marsh	Sunflowers (*Helianthus* sp.) Hemp Greater ragweed Bluegrass	4 ft. 3 in.	None
9	Nov. 13	Rolling	1	Northwest	Unknown	200	Drainage Ditch	Smartweed (*Polygonum* sp.) Lesser ragweed(*Ambrosia artemisiifolia*)	1 ft.	Heavy (closely grazed)
10	Nov. 15	Level	2	South North	Badger *Taxidea taxus taxus*	10	Roadside Ditch	Reed (*Phragmites* sp.) Goldenrod (*Solidago* sp.) Reed Bluegrass	4 ft. 5 in.	None
11	Nov. 20	Level	1	Northwest	Badger	220	Pothole	Bluegrass Greater Ragweed Sunflowers Wild Rose (*Rosa* sp.)	5 in. 4 ft.	None
12	Nov. 27	Hilly creek	2	All west	Woodchuck	200	Creek	Bluegrass	2 in.	Heavy

* No differentiation is given to numbers present in den.

** Pre-hibernation den environment refers to period of den selection for hibernation and preparation for hibernation.

foxes each dug two, or 16.67 per cent. The origin of one den was unknown. Figure 1 shows a fox den, den No. 7, which was utilized by skunks.

The average distance of the dens from water was 285.83 yards. The four dens near Skunk River averaged 540, the two near Squaw Creek 320 yards, and the three near Little Wall Lake 66.66 yards from water. Three other dens were 200, 200, and 10 yards respectively from a pothole, drainage ditch, and a roadside ditch.

The location of these dens was rather equally divided between wooded creek grazing land and other untilled land, as five, or 41.67 per cent, were on the above mentioned grazing land and the rest on untilled areas. The land on which three dens were found was moderately grazed and that on which one den was observed was heavily grazed. Five of the seven dens on the untilled land were in fencerows and the other two in weed-patches at distances of approximately 250 and 300 yards from the fencerows.

Fig. 1. Den No. 7—A fox-dug den.

Bluegrass was the predominant vegetation at the dens on the grazing land, but hemp and ragweed were also very evident as cover, in several instances to the extent of being almost as dominant as the bluegrass. At the dens on the untilled land ragweed, hemp, bluegrass, and dropseed were all more or less evident. The bluegrass at den No. 1 was closely grazed, but the hemp grew to a height of six feet. At den No. 12 the bluegrass had an approximate height of six inches. Vegetation was about one foot tall at den Nos. 6, 7, and 8 which were on an ungrazed preserve and at the other dens the predominant vegetation varied from two to five feet in height. In general, in all instances except that of den No. 12, it was difficult to note the emergence of a skunk from a den at a short distance.

Pre-hibernation den environment refers to period of den selection for hibernation and preparation for hibernation.

TABLE 2

Den Environment of Individual Striped Skunks in the Spring and Summer of 1937.

Den No.	Date First Observed	Land Site	No. of Entrances	Entrance Direction	Type of Den	Distance from water	Type of Water	Vegetation Predominant species	Average Height	Amount of Grazing
13	March 31	Rolling	2	both North	Fox	220(yds)	Pothole	Bluegrass	No new growth	None
14	April 14	Hilly	1	Southeast	Wood-chuck	80	River	Bluegrass Sunflowers	No new growth	None
15	Aug. 3	Rolling	1	Southwest	Unknown	100	Drainage Ditch	Smartweed Lesser Ragweed Sweetclover	1 ft.	Heavy Grazing
16	Aug. 4	Level	2	East West	a culvert	220	Farmyard	Alfalfa (Medicago sativa) Foxtail (Setaria sp.) Smartweed	18 in.	None
17	Aug. 7	Hilly creek	1	North	Wood-chuck	440	River	Bluegrass Hemp Smartweed	3 in. 4 ft. 2 ft.	Heavy Grazing
18	Aug. 7	Hilly creek	1	West	Wood-chuck	440	River	Bluegrass Hemp Smartweed	3 in. 4 ft. 2 ft.	Heavy Grazing
19	Aug. 7	Hilly creek	1	Northeast	Hollow log	440	River	Hemp Smartweed	6 ft. 4 ft.	Heavy Grazing
20	Aug. 9	Hilly creek	3	Northeast Northwest Southwest	Wood-chuck	300	Creek	Bluegrass Lesser Ragweed	5 in. 3 ft.	Heavy Grazing
21	Aug. 10	Rolling	2	Northeast North	Badger	440	Creek	Lesser Ragweed Greater Ragweed Pigweed (Amaranthus retroflexus) White sweetclover	2 1/2 ft.	None
22	Aug. 10	Rolling	2	Southeast Northwest	Badger	440	Creek	Same as above but with immediate predominant being Greater Ragweed	3 1/2 ft.	None
23	Aug. 10	Hilly creek	1	Southwest	Wood-chuck	200	Creek	Bluegrass Wild Rye	2 ft.	Heavy

Den Environment of Individual Striped Skunks in the Spring and Summer of 1937

Comparing the environment of these dens with those in the autumn it is evident that a higher percentage were found on rolling or hilly creek land. Of the eleven dens listed in Table 2 ten, or 90.91 per cent, were found on the above mentioned creek land. Further comparison shows more of a balance of dens used with single and several entrances in the spring and summer than in the autumn. Six, or 54.55 per cent, of these dens had only one entrance and the remaining five had several entrances.

Woodchucks dug five, or 45.46 per cent, of the dens; badgers two, or 18.18 per cent; and, foxes one, or 9.09 per cent. The origin of one den was unknown, a culvert was used as another den, and a hollow log as a third. Figure 2 shows the culvert in a fencerow and figure 3, a badger-dug den. Tall, heavy vegetation grew around the culvert and almost completely covered it. This is rather typical of cover in fencerows through which a number of animals aid in making a pathway and later use it, including the striped skunk. Evidence of the latter using these pathways is presented by scat collection by Selko (1937).[3]

The average distance of the dens from water was 301.82 yards, which average was closely comparable to that of the dens observed in the autumn. The average distance of four dens from Skunk River was 350 yards, and of four others from Squaw Creek was 345 yards. The other dens were 220, 100, and 200 yards, respectively, from a pothole, drainage ditch, and a farmyard where water was obtainable.

As in the autumn the location of the dens was quite equally divided between wooded creek grazing land and other untilled land. Six, or 54.55 per cent, were on wooded grazing land along a creek and the remainder were on untilled land. Areas of wooded creek grazing land on which four dens appeared were heavily grazed. Of the dens away from the woodland only one, den No. 14, was on grazed land and this area was heavily grazed. Figure 4 shows a woodchuck-dug den which was used by skunks on wooded creek grazing land. One of the dens on untilled land was in a fencerow and the others were at distances of 40, 75, 40, and 60 yards from fencerows.

Bluegrass, hemp, and greater and lesser ragweed were predominant in the wooded creek grazing land the lesser and greater ragweed and hemp were predominant with smartweed and foxtail often very evident.

Den Environment of Striped Skunk Families in the Spring and Summer of 1937

Family dens, as in the autumn den environment and spring and summer den environment for individual skunks, were mainly found in hilly or rolling

3 Selko, Lyle F. Food Habits of Iowa Skunks in the Fall of 1936. Jour. Wildlife Mgt. **1**(3-4):70-76.

land. Six, or 85.71 per cent, of the family dens listed in Table 3 were located in hilly or rolling land, and only one on level land. All of these dens had two entrances with three opening to the southeast, three to the east, two to the south, two to the northeast, one to the north, and one to the northwest.

A very decided difference was noted between these dens and the previously discussed ones in type and location. Four, or 57.14 per cent, of the dens were dug by skunks and three of these, or 42.86 per cent, were on cropped land. Neither skunk dug dens or those on cropped land have appeared in the previous den environment investigation. Of the other dens used by skunk families two, or 28.57 per cent, were dug by woodchucks; and one, or 14.29 per cent, was a dry tile drain. Of the remaining four dens three, or 42.86 per cent, were located on untilled land; and one, or 14.28 per cent on wooded

Fig. 2. Den No. 16—A culvert lying in a fencerow.

Fig. 3. Den No. 21—A badger-dug den. As this was taken on April 10, the characteristics of the vegetation in Table 2 are not present.

TABLE 3

Den Environment of Striped Skunk Families in the Spring and Summer of 1937.

Den No.	Date First Observed	Land Site	No. of Entrances	Entrance Direction	Type of Den	Distance from water	Type of water	Vegetation Predominant species	Average Height	Amount of Grazing
24	May 8	Low to rolling	2	Southeast Northeast	Skunk	440(yds)	Pothole	Slough grass (Spartina sp.) Sunflowers		None
25	June 25	Level	2	North Southeast	Skunk	175	Farmyard	Bluegrass Alfalfa	6 in.	None
26	June 26	Level to gently rolling	2	East South	Skunk	300	Farmyard	Alfalfa	6 in.	None
27	Aug. 3	Rolling	2	Southeast Northwest	Skunk	880	Creek	Oats (Avena sativa)		None
28	Aug. 10	Rolling				880	Tile Drain	Smartweed (Polygonum persecaria) Milkweed (Asclepias sp.) Pigweed White sweetclover	36 in.	None
29	Aug. 13	Hilly	2	East East	Wood-chuck	200	River	Dropseed grass Smooth sumac (Rhus glabra) Grapevine (Vitis sp.)	1 1/2 in. 5 ft.	None
30	Aug. 19	Hilly	2	South Northeast	Wood-chuck	100	Small creek	Hemp Goldenrod (Solidago sp.)	3 ft.	Heavy

creek grazing land. Figure 5 shows a skunk-dug family den, in an untilled area, a slough.

The average distance of these dens to water was 425 yards. Two were 300 and 175 yards from available water at farmyards; others were 440, 880, 100, 200, and 880 yards, respectively, from a pothole, Squaw Creek, a small creek, Skunk River, and a wet tile drain.

Dominant vegetation showed no consistency in being the same around all dens in the family studies because of considerable variation in the den location. Also, much variation occurred in the average height of vegetation, the range being from six-inch bluegrass to smooth sumach five feet tall. There was grazing and that heavy, on only one area where den No. 30 was observed.

The preference of the skunk family for den vegetative cover over barren environs has the support of observations at three dens. The first observation was at den No. 27. The skunk family here evacuated within several days after the harvesting of the oats which surrounded their den. At den No. 30

Fig. 4. Den No. 12—A woodchuck-dug den along Squaw Creek, on April 17, showing wooded creek grazing land in the background.

Fig. 5. Den No. 24—A skunk-dug den in a slough on May 19 with the predominant vegetation of the past year's slough grass and sunflowers surrounding it.

the same thing happened when the hemp and goldenrod were mowed. Den No. 28 had two entrances from the rockpile, one to the east and one to the west. Smartweed, pigweed, and white sweet clover surrounded both entrances. Only the entrance to the east had been used all summer. The farmer, who tilled the land on which this rockpile was situated, used a scythe to cut the weeds very close to the ground at the east side of the rocks which was next to his cornfield. He did not cut those on the other side which were adjacent to the fence. The entrance at the east was abandoned and the one at the west became the front door.

Summary

The majority of dens observed occupied by skunks were in hilly or rolling land. There were approximately twice as many dens with single entrances as with several entrances used in the autumn, during pre-hibernation activity. Individual skunks in the spring and summer used as many dens with one entrance as with two, whereas all the family dens noted by the writer had two entrances.

In the autumn, 58.33 per cent of the dens used were of woodchuck excavation. Individual skunks in the spring and summer used woodchuck dens to the extent of 45.46 per cent. Skunk families were found more in skunk-dug dens than woodchuck-dug dens to the extent of 57.14 per cent of the total number of family dens.

No active dens were located over one-half mile away from water, but probably some were utilized that were further away also. The majority of these dens were located near rivers and creeks.

In the autumn, 41.67 per cent of the dens were on wooded creek grazing land and 58.33 per cent on untilled areas. In the spring and summer 54.55 per cent of the individual skunk dens were on wooded creek grazing land and 45.45 per cent on untilled land. Almost half, or 42.86 per cent, of the dens used by skunk families were on cropped land, and all of these on cropped land were of skunk construction. There were 42.86 per cent of the family dens also on untilled areas, and only 14.28 per cent on wooded creek grazing land.

The predominant cover at dens in the autumn and dens occupied by individuals in the spring and summer on the wooded creek grazing land was usually bluegrass, but lesser and greater ragweed and hemp were always evident, in several cases being almost as dominant as the bluegrass. The predominant vegetation at the autumn dens and dens occupied by individuals in the spring and summer on untilled land was usually lesser and greater ragweed and hemp, with bluegrass and dropseed occasionally more or less evident. At the skunk family dens the predominant vegetation varied with the varied den location. Dens were found in small grain, alfalfa, and hayland fields, and in slough and other untilled areas.

Cover at all den entrances, except one, was tall enough to furnish good concealment if any was desired. Three instances were recorded where cover was removed at skunk family dens. At two of the dens the families moved out, and at the third, a den under a rockpile, the entrance was changed to the opposite side of the rocks where cover was plentiful.

Breeding of the Cottontail Rabbit in Southern Michigan

Durward L. Allen

The recorded information on the breeding of cottontails is more limited than might be expected from the wide distribution and abundance of this subspecies *(Sylvilagus floridanus mearnsii)* and its allies. Audubon and Bachman (1849) wrote that in the northern states they have about three litters per season with from five to seven young per litter. Kennicott (1857) concluded, from studies in Illinois, that young are produced three or four times a year and that there are usually from four to six at a birth. Evermann and Clark (1911) stated that in northern Indiana the rabbit breeds at least twice in a season, producing one litter in early spring and another in July or even as late as September. Seton (1929) said that there are three or even four mating times a year. "The young are in number 4 to 6 or 7, very rarely as many as 8, or as few as 3." Trippensee (1936) believes that in Michigan there are at least two broods per season and possibly four. The average number of young in 27 litters was 5.04. The maximum was eight.

The gestation period of the cottontail is not definitely known. Seton points out that from analogy a period of about 30 days is to be expected. Dice (1929) experimented with cage-bred *Sylvilagus floridanus alacer* and concluded that on a basis of somewhat insufficient evidence the gestation period of that subspecies was probably 28 days or less.

The following records were obtained in the course of an ecological investigation* at the W. K. Kellogg Bird Sanctuary and Farm in Kalamazoo County, Michigan. This area of farmland is 500 acres in extent and contains a pit lake of about 20 acres. Plantations of conifers and extensive natural brush coverts make the territory very favorable to cottontails.

Breeding Season

A total of 11 litters of young rabbits were examined in the course of this work. Of these, two litters were in the nest and 9 were in the embryonic stage. The average number of young in this series was 5.1. In Table 1 are given the results of 20 autopsies on female rabbits during late winter and spring of 1935, 1936, and 1937. It will be seen that of eight females examined in January and February only one was pregnant. This autopsy on February

* A study made by the Game Division of the Michigan Department of Conservation from September, 1935 to August, 1937. The area is owned and operated by Michigan State College. A few records included from the spring of 1935 were incidental to studies under a fellowship in zoology at the Kellogg Bird Sanctuary.

21, 1936 is the earliest breeding record obtained in this study. Trippensee (1936) gives records to show that breeding occurs much earlier than this. He quotes one report for southern Michigan of four pregnant females on January 25, 1933. The same author found a nest of young near Ann Arbor on March 24, 1932. My earliest record for young rabbits out of the nest is April 4, 1936. A neighbor's cat brought in a dead one on this date, and on April 28 it obtained another which it brought in alive. The first young out of the nest normally were seen on April 30 in 1935, April 17 in 1936, and April 20 in 1937. The latest indication of breeding date obtained in this study was a young rabbit evidently just out of the nest seen during the last week in July, 1936. Other investigators have found evidence that breeding sometimes occurs even later in the season. Dice (1920) found four 70-millimeter embryos in a female autopsied on July 21, 1919. Trippensee (1936) quotes a record from R. E. Yeatter of a nest of young as late at September 30.

In three years of observation at the Kellogg Farm it appeared that most of the breeding and bearing of cottontails occurred during the six months period from February to July inclusive. Although coition may at times take place during January and young may be born after July, it is very improbable that much early and late breeding occurred during this study on the area discussed. Field work was intensive during two years and had many young indicative of such breeding been present, there is a good chance that at least a few would have been observed.

Nesting and Care of Young

While occupied by the young, most rabbit nests are nearly invisible and hence very difficult to find. Several empty nests were discovered but only two had the litter still present. One of these, which was dug out by workmen, was located under the leaves in a pocket in a low bank near the edge of the lake on April 18, 1935. The ground was disturbed and the mother evidently never returned. The five young were dead on the following day. This hollow was about 4 inches deep and carefully lined with rabbit fur and bits of dry leaves. It was covered with fur, leaves, and grass. The mat of fur and grass that usually covers rabbit nests is very effective both for concealment and shelter. I have on two occasions examined nests of young after a protracted rain and found them to be dry and warm.

Much better records were obtained from a nest on the lawn near the laboratory at the sanctuary. It was first noticed by Dr. M. D. Pirnie on the morning of April 3, 1937, beside a ground juniper near the drive. This nest was shaped roughly like a shoe, having the opening at one end, and consisted of a tunnel about 8 inches long extending under the sod. It was lined with grass, and at first the freshly dug earth, which made discovery possible, was conspicuous beside the hole. The nest was covered with a mat of rabbit fur and oak leaves. The young were blind, helpless, and thinly covered with short sparse hair when first found. They were disturbed as little as possible, but on the second day one was removed and weighed. On this date (April 4)

it weighed 46.2 grams. On April 9 one of the young, selected at random, weighed 72.5 grams. By this time the fur was thick and brown. The eyes of these rabbits were first open on April 13, or ten days after the nest was found. On this date one of them weighed 89 grams. These young were in the nest every day until April 18. They evidently left during the night of April 17 and did not return.

Seton gives the weight of a new-born Kansas cottontail as 24 grams. The average weight of nine still-born Michigan cottontails examined by Trippensee was 32.8 grams. As the young rabbit in the aforementioned nest weighed only 46.2 grams on the second day after discovery, it is doubtful whether this brood was more than a day and a half old when the nest was found. It appears probable that they were born on the night of April 1. If this is true, the eyes of these young rabbits opened on the eleventh day and left the nest on the sixteenth day after birth.

This nest was well situated to be under fairly close observation. The mother was never seen near it in daytime. Several times, however, a rabbit was observed close to the nest at dusk or after nightfall.

On April 20, two days after the nest was found empty, two very young cottontails were seen less than 100 feet from the site of the nest. From their size it appeared very probable that they belonged to this litter. One of these juvenals was seen nearly every day until June, as it lived under the junipers in front of the laboratory and fed upon wheat and grass in the peafowl pen located there. It was often out at any hour in the daytime but was usually seen in late afternoon and evening. This young rabbit became quite tame and could be approached to within a few feet. It showed no fear of the peafowls and often fed within easy pecking distance of these birds. On May 27 at 5:30 p. m. a box trap was set in the junipers 20 feet from where the rabbit was feeding. In an hour it was in the trap. Its weight on this date was 463.8 grams. If this rabbit was one of those from the nest, it was probably very near 56 days old. This agrees fairly well (for a rabbit that has fed upon wheat and laying mash) with Trippensee's (1934) growth curve, which indicates that a rabbit eight weeks old should weigh about 400 grams.

Trippensee (1936) states that the growth of young cottontails is rapid and that they may make limited excursions out of the nest and eat grass when two weeks old. Burroughs (1900) tells of finding a rabbit nest on a newly mowed lawn. The young scattered from tht nest once but were back again the next day. Although the rabbits from the nest on the sanctuary may have been out and returned at night, it is quite certain that they never returned after the nest was found empty on April 18. As to subsequent care by the mother, Seton says, "She may suckle them individually when she meets them during the few days following the dispersal; but there is no evidence to show that she ever gathers them together, or cares for them as a brood, after once they have left the nest."

In this respect I had an opportunity to make some pertinent observations in Ann Arbor, Michigan, during May, 1929. A rabbit nest with four young

had been located on the lawn of a fraternity house. The nest was a shallow pocket in the sod, lined with grass and covered with a mat of fur and grass. It was quite invisible from a distance of six feet. One morning the nest was empty, the young having left during the preceding night. As the lawn was very large and open, the only cover within fifty yards in any direction was formed by some well-spaced shrubs. Investigation disclosed that in three of these clumps a single young rabbit was crouched down in the oak leaves lodged among the stems. Two of the rabbits were twenty yards apart and the other was about 30 yards from the nearest of these. The fourth animal was not found. They were returned to their hiding places and on the following day one of them was again located in a shrub; but after this none was seen. Whether the young had found this cover independently or whether the mother had been instrumental in hiding them is not indicated, but these juvenals were definitely scattered on the day following their abandonment of the nest.

Sex Ratio

Probably the largest series of rabbits of which the sexes are known is that of Gerstell (1937), who examined 6,394 animals caught in live traps in Kansas and shipped to Pennsylvania for restocking purposes. Of these 50.8 percent were females and 49.2 percent were males. In a sample of 93 rabbits, taken by box trapping at the Kellogg Farm during the fall of 1936 before any shooting was done, 48 were males and 45 were females, giving a sex ratio of 0.483 females to the total number sexed. Records obtained by M. B. Trautman (Trippensee, 1934) in Ohio, and Gerstell in Pennsylvania indicate that female rabbits are more likely to hole up during cold weather than males. Thus the sex ratio among animals taken by shooting in winter may not be a reliable index of the ratio existing in the population. On the area discussed there was a tendency for more male rabbits than females to be shot on cold days. However, in the total of 383 rabbits sexed in this study, which were taken by trapping, shooting, and other methods, 195 were males and 188 were females; giving a ratio of 0.49.

Summary

In eleven litters of cottontail rabbits from Kalamazoo County, Michigan, the average number of young was 5.1. The regular breeding season lasts from February through July, although some breeding evidently occurs earlier and later than this. Records from one nest showed that the eyes of the young rabbits opened on about the eleventh day and they left the nest on about the sixteenth day. If the gestation period of the cottontail is roughly one month and the young are cared by the mother for 16 (or a few more) days, 50 days would encompass the length of time needed for producing a litter. A six-month breeding period, then, would easily allow time for a female to bear and rear to self-sufficiency three sets of young. However, on a basis of 12 autopsies during February and March, it appears that most females breed during the latter month. In one case breeding was probably deferred until April. If these dates are representative, it appears probable that in this region females ordinarily produce two litters per season. Young rabbits of two litters scattered after leaving the nest and there was no evidence of further association

as a family. The sex ratio in a series of 383 rabbits taken chiefly by box trapping and shooting was 0.49 females.

TABLE 1

Rabbit Litters as Recorded from Nests and Breeding Season Autopsies on Females

Date	No. of Young	Size	Evidence
1/10/37	–	–	Not pregnant
1/13/37	–	–	Not pregnant
1/18/37	–	–	Not pregnant
2/17/37	–	–	Not pregnant
2/17/37	–	–	Not pregnant
2/19/37	–	–	Not pregnant
2/21/36	5	4 mm	Embryos
2/28/37	–	–	Not pregnant
3/ 1/37	–	–	Not pregnant
3/ 3/37	6 (?)	Minute	Uterine enlargements
3/ 3/37	–	–	Not pregnant
3/12/37	4	3 mm	Embryos
3/16/35	4	11 mm	Embryos
3/17/37	5	3.5 mm	Embryos
3/23/36	5	13.5 mm	Embryos
4/ 3/37	5	–	Young in nest
4/10/35	4	–	Embryos
4/18/35	5	–	Young in nest
4/19/36	7	7 mm	Embryos
5/17/37	7	21 mm	Embryos

Average number of young in 11 litters—5.1.

REFERENCES

AUDUBON, J. J. AND J. BACHMAN. 1849—The quadrupeds of North America. Geo. R. Lockwood, New York, 3 vol.

BURROUGHS, JOHN. 1900—Squirrels and other fur-bearers. Houghton Mifflin Co., New York, 1-149 pp.

DICE, L. R. 1920—The mammals of Warren Woods, Berrien County, Michigan. Univ. Michigan Mus. Zool. Occ. Papers **86**:1-20.

———1929—An attempt to breed cottontail rabbits in captivity. Jour. Mamm. **10**:225-229.

EVERMANN, B. W. AND H. W. CLARK. 1911—Mammals of the Lake Maxinkuckee region. Washington Acad. Sci. Proc. **13**:1-34.

GERSTELL, RICHARD. 1937—Management of the cottontail rabbit in Pennsylvania. Pennsylvania Game News **7**(12):6-7, 27, 30.

KENNICOTT, ROBERT. 1857—Quadrupeds of Illinois injurious and beneficial to the farmer. Ex. Doc. 32, 35th Congress, 1st Session: Comm. Patents Rept. 1857. Agriculture. Washington 1858, 72-107 pp.

SETON, E. T. 1929—Lives of game animals. Doubleday, Doran & Co., Garden City, New York, 4 vol.

TRIPPENSEE, R. E. 1934—The biology and management of the cottontail rabbit. Univ. Michigan School of Forestry and Cons. Unpub. Thesis, 1-217 pp.

———1936—The reproductive function in the cottontail rabbit (*Sylvilagus floridanus mearnsii* Allen) in southern Michigan. North Am. Wildl. Conf. Proc., 344-350 pp.

GAME DIVISION,
DEPARTMENT OF CONSERVATION,
LANSING, MICHIGAN.

Fig. 1. Rabbit nest with coverlet of fur drawn aside. The young are hidden beneath the sod. Fig. 2. Litter of young rabbits approximately 11 days old. Fig. 3. Young rabbit approximately 8 days old. Fig. 4. Young rabbit at nest on the day its eyes opened (removed from the nest for photographing).

Book Reviews

VERGLEICHENDE MORPHOLOGIE DER NIEDEREN PFLANZEN. Eine Einführung in deren Formbildung und Formwechsel auf entwicklungsgeschichtlicher Grundlage. Von Bruno Schussnig. Erster Teil: Formbildung. Gebrüder Borntraeger, Berlin. 1938. viii + 382 pp., 470 figs. RM 38.00.

A conspicuous increase of interest in the lower plants in recent years is attested by a fairly large number of excellent treatises of various groups. The lower plants (Proto- and Thallophyta) had not, however, been presented as a whole on a distinctly "comparative" basis; hence, this viewpoint distinguishes the present work from previous ones and claims for it an outstanding position in the available literature.

Part I of the "Vergleichende Morphologie der niederen Pflanzen" is devoted to the comparative morphology of the cell, the cell as the elementary organism and as the elementary unit, comparative organography of lower plants, and comparative anatomy of the thallus. Part II, which is to follow soon, will treat of the phenomena of reproduction, alternatiion of generations and nuclear phases, sexuality, and inheritance and phylogeny. It will contain the bibliography and indices of both parts.

According to the author, the heterogeneous nature of the subject precludes a truly typological treatment, which is also made impossible by the phylogenetically separated levels of the unicellular Protophyta and the multicellular Thallophyta. Consequently, the comparative treatment aims to trace the course of development followed by these groups. In other words, the point of view is definitely phylogenetic. This makes for the unity of presentation so necessary here and explains the author's need for certain new collective terms or the reapplication of others to fit new meanings. The reader is greatly assisted by the large number of splendid illustrations, many of which are original. The subtitle "Introduction" is readily understandable, in view of the large amount of information to be considered, and yet seems modest in comparison with other works. Students of lower plants will certainly use this informative and highly stimulating book to great advantage.—TH. JUST.

MANUAL OF PTERIDOLOGY. Edited by Fr. Verdoorn. Martinus Nijhoff, The Hague. 1938. xx + 640 pp., 121 figs. 24 guilders.

Bryophytes and Pteridophytes are often classified together as Archegoniates. On this basis it is quite natural that the editor of the "Manual of Bryology" should follow it up with a companion volume devoted to the Pteridophytes. The works are actually quite similar in character, both being composed of "a collection of essays" without aiming at exhaustive treatment of the literature on hand. Although primarily conceived to assist the taxonomist in broadening his knowledge the "Manual" can and will be profitably consulted by botanists with other interests. The "Manual of Pteridology" covers in 23 chapters, contributed by specialists, all aspects of our knowledge of Pteridophytes ranging from morphology, anatomy, cytology, physiology, ecology, geographic distribution to the classification of living and extinct groups and their phylogeny. As is unavoidable in such a composite work the views of some contributors do not exactly coincide. But this circumstance reveals at least tthe various possible views available and emphasizes the need for further illuminating research. A deplorable "lapsus calami" (pp. xvi, xvii) is the designation of haplonts, haplo-diplonts, and diplonts as haplobionts,

haplo-diplobionts, and diplobionts respectively. This confusion could easily be avoided in future by the adoption of G. M. Smith's recently proposed terms: biphasic (haplobiontic) and triphasic (diplobiontic). Taken as a whole the "Manual" gives an excellent cross section of the ascertained knowledge as well as a good picture of the many pending problems. Thus it is indispensable in all work on Pteridophytes.—TH. JUST.

HANDBUCH DER PALÄOZOOLOGIE. Herausgegeben von O. H. Schindewolf. Lfg. 1: Gastropoda, von W. Wenz, Bd. 6, Teil 1: Allgemeiner Teil und Prosobranchia, viii + 240 pp., 471 figs. Gebrüder Borntraeger, Berlin. 1938. Subscription price RM 36.00, paper bound; single copy RM 45.00.

While paleobotanists are fortunate in having at their disposal several major treatises of fairly recent date paleontologists and zoologists have for some time been in dire need of a large collective work recording the present status of our knowledge of fossil animals. The appearance of the first installment of the "Handbuch der Paläozoologie" represents therefore a landmark in the history of paleontology. It is fittingly dedicated to the memory of Karl Alfred von Zittel whose classical work had held the field for some 60 years, and to Ferdinand Broili, Zittel's successor. The first plan of the work was elaborated in 1930 and the intervening years represent a necessary preparatory period which, it is hoped, will facilitate the rapid publication of the individual parts. The editor of this colossal undertaking, which is contemplated in 20 volumes, enlisted a large number of specialists as contributors thus ensuring the highest possible standards of treatment. For obvious reasons the work will have a predominantly taxonomic character although all other aspects of fossil animal life are to receive proper attention and space. All systematic categories as far as the genera and subgenera are concerned are to be included. In view of the widely scattered sources of information the task is tremendous. That however, proves definitely the great need for such a praiseworthy venture. The first part gives evidence of the excellence to be expected of this truly monumental work.—TH. JUST.

ELIMINATION UND SELEKTION. Eine Untersuchung über Merkmalsprogressionen bei Tieren und Pflanzen auf genetisch- und historisch-chorologischer Grundlage. Von W F. Reinig. Gustav Fischer, Jena. 1938. viii + 146 pp., 29 figs. Paper bound RM 8.00.

Reinig recently pleaded for the establishment of a specific chorologic methodology indispensable in exact biogeographic research, despite the fact that biogeography is obliged to use, in a large measure, the results and methods of other branches of biological knowledge. In the present work he goes beyond the analyses of the dynamics of distribution by the adoption of genetic methods to attempt the "analysis of the directed geographic variability of characters." Part I presents the historic and genetic chorological background, e.g. polytopous and monotopous origin of systematic categories, the constancy of the ecological valence of species, diluvial biotops of the holarctis; Part II discusses the dynamic chorologic basis of variability, e.g. causes of postglacial migrations, limits of these; Part III evaluates critically the older and newer "climatic rules"; Part IV contains the conclusions reached in the previous chapters and states clearly the author's views. "Elimination" is defined (p. 59) as the "diminution of the complement of allels, due to individual migrations and independent of selection, proceeding from the center of the area or distribution, respectively, to the absolute limits of the area" and is claimed to be active as an evolutionary factor in addition to mutation and selection. The critique of old theories and the large body of new information and views give the book a definitely provocative character and recommend its serious study.—TH. JUST.

THE ORIGIN OF LIFE. By A. I. Oparin. Translation with annotations by Sergius Morgulis. Macmillan, New York. 1938. ix + 270 pp., 8 figs. $2.75.

Despite the paramount and age-old importance of the problem of "the origin of life" few scientists are actually engaged in work devoted specifically to it. The present volume attempts to summarize the existing information and to present the author's own views based on extensive work. The latter he has done well and in a provocative manner. The presentation of the available information however is not so complete for the extremely pertinent work of W. D. Francis (e.g. "Iron as the original basis of protoplasm," Brisbane 1935) and the relevant theory of H. A. Gray and N. M. Bligh ("The origin of living matter," Cambridge 1933) receive no attention to mention only two cases. Other notable deficiencies are found in a perusal of the "Bibliography", e.g. H. G. Bungenberg de Jong appears as "Budenberg de Jong." It seems that such discrepancies and omissions could have been avoided profitably since they lessen considerably the reliability and value of an otherwise highly stimulating book. The frequent references in this volume (as well as in certain other recent scientific books) to political leaders as scientific authorities are likewise not commendable. On the whole the book represents an earnest though by no means exhaustive effort towards the furtherance of our knowledge of the nature of life.—TH. JUST.

CHARLES DARWIN: A PORTRAIT. By Geoffrey West. Yale University Press. New Haven. 1938. xv + 359 pp., frontispiece, 7 pls. $3.50.

The existing literature on Charles Darwin is indeed impressive. Consequently it might seem superfluous to add another biography, were it not for the new "portrait" presented. Darwin is here shown as "what he was," with his whole background dating from the eighteenth century and representing with his family and friends "some of the best elements of English life in their period." Appended is "Book Four: Commentary" in which Darwin's work is examined critically regarding its influence on biological thought and life in general. Although this part must of necessity be brief, it offers highly suggestive reading and illustrates clearly the universal impact of Darwin upon his and following generations. A select bibliography concludes the volume. The warmly human touch of this portrait contributes much towards a better understanding of Darwin, the man.—TH. JUST.

FOREST TREES OF THE PACIFIC COAST. By Willard Ayres Eliot, assisted by G. B. McLean. G. P. Putnam's Sons, New York. 1938. 565 pp., 248(249) figs. $5.00.

This last addition to the well known series of Putnam's Nature Books represents an attempt to bring up to date Sudworth's "Forest Trees of the Pacific Slope" without being a second edition of it. The range covered by the "Forest Trees of the Pacific Coast" is large, e.g. Alaska through British Columbia to Washington and Oregon. On account of the wide distribution of many species it could also be used in Idaho, northern California and eastward to the western slopes of the Rocky Mountains. It was the aim of the author to meet the demands of the many nature lovers who want a convenient book for identification "at sight" which is still scientifically sound and accurate. This aim seems to be well met. The large number of splendid photographs (here preferred to drawings) will certainly add to its popularity.—TH. JUST.